

RAPTOR AND WADING BIRD MIGRATION IN VERACRUZ, MEXICO:
SPATIAL AND TEMPORAL DYNAMICS, FLIGHT PERFORMANCE,
AND MONITORING APPLICATIONS

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by
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MAY 2007

The undersigned, appointed by the Dean of the Graduate School, have examined the dissertation entitled

RAPTOR AND WADING BIRD MIGRATION IN VERACRUZ, MEXICO:
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AND MONITORING APPLICATIONS

presented by ERNESTO RUELAS INZUNZA

a candidate for the degree of DOCTOR OF PHILOSOPHY

and hereby certify that in their opinion it is worthy of acceptance.

To my late mother, Linda Inzunza Sáinz, for the spark; my friends and colleagues
Laurie J. Goodrich, Stephen W. Hoffman, and John Faaborg, for the means;
and my children, Isabela and Santiago, for their love.

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I want to express my deepest appreciation for John, who gave me the opportunity to join his Avian Ecology Lab as a graduate student. Over the years, he became a good friend as well, and did many things for me and my family, for which I owe him a lot more than academic advice. Perhaps the best example of his care for me and my work is what happened in the fall of 2003, when him and Janice gave me their beloved “TEX 2NZ” red pick-up truck to help me complete my last two field seasons of work (and for those who knew John’s affection for his truck, this was the equivalent of a person giving an arm away).

This dissertation has had the contribution of many people. I should emphatically say that, if a project deserves to be called a ‘collective project,’ this is certainly it. I would love to take the time and space to give every single person his/her credit for making it happen, but it would not be possible without pages and pages of text.

The Veracruz River of Raptors Project (VRR), a cooperative effort between Pronatura Veracruz, Hawk Mountain Sanctuary, and HawkWatch International, is a conservation initiative whose mission is the conservation of migratory raptors, wading

birds, and their habitats as part of the local biodiversity, through environmental education, research, monitoring, and habitat conservation. VRR was conceived over a several months, in conversations with Steve Hoffman inside a large tent in the Goshute Mountains of Nevada in the fall of 1989. These conversations continued one year after, when Laurie Goodrich and I sat in Hawk Mountain's library and put together a short proposal that received immediate support from her, Steve, and Jim Brett.

In spring of 1991, we assembled the first field team and collected data over 60 days in several localities along a transect that ran along a west to east axis following Federal Highway 140 between La Antigua and Xalapa. Since then, we have had field crews covering the migration continuously, and to this date (November 2005) we have collected data during 17 field seasons, and plan to continue this work over long-term.

In subsequent seasons, when we became aware of the importance of this locality for migrating raptors, we developed other aspects of this project. In 1992, Evodia Silva Rivera developed the first education materials for teachers and elementary school children. In that same field season, we ran a trial raptor banding station in El Palmar, with meager results.

In 1994, when I was hired by Pronatura Veracruz as its executive director, I brought the VRR Project under the umbrella of conservation activities of Pronatura. Laurie Goodrich and Sharon M. Gaughan brought a first Hawk Mountain birding tour in the fall of 1994, and started an ecotourism program to help raising funds for VRR. The next year, we launched a membership program in support of the project, called "Amigos del Río de Rapaces."

In 1995, Sandra L. Mesa Ortiz, Sharon M. Gaughan, and Liliana Coronado Limón re-designed all the education materials and launched a very ambitious environmental education program that, to this date, runs parallel to our monitoring work. They also coined the motto “Veracruz River of Raptors” for our project. In 1997, Karen L. Scheuermann magically appeared to rescue the idea of the banding station and, out of a tremendous personal effort, ran the banding station in La Mancha for several years and trained numerous local field biologists to band hawks. Robert Straub did a first pioneer passerine count in the fall of 1999 in La Mancha, very close to Eduardo Martínez Leyva who ran a first passerine banding station there. Rafael Rodríguez Mesa started the job of identifying key critical habitat for stopover migrants in 2000.

Besides those initial efforts, we have also had many individuals playing the critical role of “stabilizing” all this work over long term and sustaining its quality. Jorge E. Montejo Díaz, Octavio G. Cruz Carretero, Ruth Tingay, Zachary N. Smith, Rafael Rodríguez Mesa, Efraín Castillejos Castellanos, and Eduardo Martínez Leyva, worked diligently as field crew leaders for the monitoring team (a complete list of field biologists is available in Appendix 2); Sandra L. Mesa and Yumei Cabrera Carrasco expanded education programs; Larry D. Maynard, James Dion, and Robert Straub continued ecotourism and membership programs; Karen L. Scheuermann, L. Fernando Rincón Ramos, Eduardo Martínez Leyva, and Alexaldo García Miranda coordinated the raptor banding station. I am also indebted to M. Martín Peñaloza Pérez, Juanita B. Sandoval Mendoza, and Norma B. Ferriz Domínguez, for their leadership and for providing administrative and emergency support for VRR when it needed it the most.

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I have saved for last a paragraph to thank the generous contribution of the Lannan Foundation, whose financial support has been essential in taking this dissertation project to completion. I am deeply and sincerely indebted to Patrick and Andy Lannan for their generosity and extend the same sincere acknowledgment to William Johnston and Mary Pat Day at the Lannan Foundation board of directors.

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RAPTOR AND WADING BIRD MIGRATION IN VERACRUZ, MEXICO:
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ABSTRACT

This dissertation is organized in four chapters that deal with different aspects of my long-term studies of migratory raptors, vultures, and wading birds, in central Veracruz, Mexico, during the course of three spring and ten fall seasons (1991-2004). The first chapter is a descriptive piece with a discussion of the role of regional topography and altitudinal distribution of thermal convection in the formation of a geographic bottleneck for soaring migrants.

I examine several characteristics (such as flocking behavior and flight mode) of an assemblage of migratory birds composed of 33 species of nine families in order to understand why these birds are funneled through this area. I also describe the magnitude of these migrations, their inter-annual variation, flocking behavior, and flight mode, and briefly discuss issues related to their stopover ecology and conservation.

One of the outstanding findings of this project is documenting the migration of over 0.8 million birds in spring and over 5.1 million in fall, the most important migratory flyway for raptors in the World. These migrations are dominated by seven species:

American White Pelican (*Pelecanus erythrorhynchos*), Anhinga (*Anhinga anhinga*), Wood Stork (*Mycteria americana*), Turkey Vulture (*Cathartes aura*), Mississippi Kite (*Ictinia mississippiensis*), Broad-winged Hawk (*Buteo platypterus*), and Swainson's Hawk (*B. swainsoni*). The migration bottleneck is a result of two features of the regional landscape. Flights are limited to the east by the Gulf of Mexico, and to the west by the availability of thermal convection. Thermal convection decreases as elevation increases, and is higher in spring than in fall. Stronger thermal convection limits our ability to record migration: it contributes to variation in geographic distribution patterns, altitude of flight, and overall conditions for migration recording.

The second chapter presents a quantitative description of the temporal dynamics of an assemblage of one species of vulture and 11 species of diurnal raptors and uses these measures of intra- and inter-annual variation to make some inferences about the effects of variables at multiple scales in species' migration patterns. I also use this information to evaluate the implications of these temporal variations on long-term monitoring schemes.

The patterns I present are a species-by-species description of spring and fall migration, and a characterization and quantification of the structural patterns of the complete assemblage. During spring, migration is unimodal in seven species and has a bimodal/unclear distribution pattern for five species. Species' migration through the region lasted between 43 and 70 days (mean=53 days). The migration season of four species is significantly shorter in spring than in the fall. I found significant differences in timing of migration across years for all species, with peak dates differing between 3-11 days. In fall, migration is unimodal for ten species. Mean duration of fall migration recorded ranges between 20-74 days (mean=52 days). The duration of fall migration was

significantly shorter than spring for five species. With no exceptions, all species had significant differences in timing of migration across years, with peaks differing between 4-9 days.

The third chapter examines the differential flight performance among species and migration seasons. I studied the behavior of nine species of large soaring birds and quantified their wing beat frequency, a commonly used measure of flight performance. There are significant differences among species' wing beat frequency, and larger birds tend to require less energetic expenditure in their flights. I also found seasonal differences in wing beat frequency in seven species, and, contrary to my predictions, spring is a season that demands higher energetic expenditure (higher wing beat frequency) for more species than fall.

My last chapter covers the topic of using of migration count data from Veracruz to assess population trends of New World vultures and diurnal raptors. I evaluated the use of migration counts to monitor populations and obtained annual estimates of population change for five species over a 10-year period. In those five species, who meet both an a priori accuracy target goal and the assumptions of a recently developed regression method, I found significant population increases.

The populations of Turkey Vulture (*Cathartes aura*), Osprey (*Pandion haliaetus*), Cooper's Hawk (*Accipiter cooperii*), Broad-winged Hawk (*Buteo platypterus*), and Swainson's Hawk (*Buteo swainsoni*) have been increasing at a rate between +1.6 and +11.1% year⁻¹ and a mean cumulative increase of 26% between 1993-2004. I was unable to assess population trends in 28 species that had very high coefficient of variation in

annual counts, less than 100 individuals recorded per field season, and/or shorter field coverage of their migration period.

What is significant in my research is the generation of baseline information on raptor, vulture, and wading bird migration ecology from one of the very few sites in the Neotropics where a long-term research and monitoring program has been sustained. This research has some immediate conservation applications, particularly the use of systematic migration counts to monitor the populations of many species.

CHAPTER 1

THE ROLE OF GEOGRAPHY AND THERMAL CONVECTION IN THE MAKING OF A BOTTLENECK OF GLOBAL IMPORTANCE FOR WADING BIRD, NEW WORLD VULTURE, AND RAPTOR MIGRATION

Abstract.- Most large, soaring, diurnal migratory birds constrain their migrations to routes defined by the combination of geographic features and weather. In this paper, I discuss the role of regional topography and altitudinal distribution of thermal convection in the formation of a geographic bottleneck for migrants. I examine several characteristics (such as flocking behavior and flight mode) of an assemblage of migratory birds composed of 33 species of nine families in order to understand why these birds are funneled through this area. I also describe the magnitude of these migrations, their inter-annual variation, flocking behavior, and flight mode, and briefly discuss issues related to their stopover ecology and conservation.

My research takes place in central Veracruz, Mexico, a location where the intersection of the Sierra Madre Oriental and the Central Volcanic Belt reduce the width of the Gulf coastal plain to a stretch of lowlands less than 40 km wide. I recorded the migration, weather variables, and observation conditions from several locations along a survey line perpendicular to the migration front, during 17 field seasons (n=4 in spring and n=13 in fall).

On average, my teams and I tracked the migration of over 0.8 million birds in spring and over 5.1 million in fall. These migrations are dominated by seven species: American White Pelican (*Pelecanus erythrorhynchos*), Anhinga (*Anhinga anhinga*), Wood Stork (*Mycteria americana*), Turkey Vulture (*Cathartes aura*), Mississippi Kite (*Ictinia mississippiensis*), Broad-winged Hawk (*Buteo platypterus*), and Swainson's Hawk (*B. swainsoni*). Although individual species of migrants select flight strategies in response to patterns of prevailing weather, most species migrate in multi-species flocks that use thermal convection and avoid crossing over water.

The migration bottleneck is a result of two features of the regional landscape. Flights are limited to the east by the Gulf of Mexico, and to the west by the availability of thermal convection. Thermal convection decreases as elevation increases, and is higher in spring than in fall. Stronger thermal convection limits our ability to record migration: it contributes to variation in geographic distribution patterns, altitude of flight, and overall conditions for migration recording. Compared to other geographic bottlenecks, central Veracruz stands out as the most important in the World.

Key words: Wading birds, vultures, raptors, migration, ecology, Veracruz, Mexico.

INTRODUCTION

Many wading and large land birds, including pelicans, ibises, herons, storks, vultures, hawks, and falcons, are diurnal migrants (Palmén 1827, Thienneman 1931). Widely accepted arguments regarding why these birds migrate during the day are intimately linked to their large size and capabilities for soaring flight. The prevalent hypotheses are that birds that: (a) Do not seek to avoid predation (Palmgren 1949); (b) Do not require large amounts of daytime to forage (Lincoln 1952); and/or (c) Can better exploit atmospheric conditions for energy-saving migrations (Baker 1978), engage in migrations that favor the choice of diurnal versus nocturnal flights.

To migrate, these birds rely on different movements of masses of air in the lower, boundary layer of the atmosphere (Arya 1988, Kerlinger 1989:70). Birds use shear wind (horizontal or advection winds of varying speed and direction), waves (irregular air displacements that follow undulating features of the landscape such as mountain ridges), and thermal convection (vertically-rising columns of warm air or 'type I' thermals) (Stull 1988, Alerstam 1990, Garrat 1992) to provide them with lift (Pennycuick 1969, 1975, Kerlinger and Moore 1989). Their movements are not random or dispersed but constrained by numerous features of the landscape, including deserts, high mountains, and perhaps most importantly, large bodies of water (Leshem and Yom-Tov 1996, Berthold 2001).

A combination of geographic features and atmospheric conditions for energy saving flights determines migration routes, and most research on the migration of diurnal soaring birds has been done along clearly identified routes (Berthold 2001). These routes can be wide or narrow depending on the combination of these variables, and some

critically narrow sections of those routes are termed ‘geographic bottlenecks,’ e.g. the end of a ‘diversion line’ such as a peninsula or an isthmus that acts as a funnel for birds reluctant to cross over water (Safriel 1968, Smith 1980, Farmer et al. unpublished).

Birds choose migration strategies in response to these extrinsic variables. They select flight modes that involve different social tendencies (e.g., from solitary to flocking), and adopt several types of ‘assisted’ flight (Lissaman and Schollenberger 1970, Pennycuik 1975, Blem 1980). Neither the extrinsic or intrinsic variables for migration are fixed properties of the landscape or the birds, and their interplay results in migration corridors that vary seasonally and flight behaviors that are highly plastic within a species (Gauthreaux 1980, Kerlinger 1989).

At geographic bottlenecks, flights are spectacular and conspicuous, and there exist very early records documenting their nature (e.g. Fernández de Oviedo 1557). Such is the case on the coastal plain of Veracruz, Mexico, where ornithologists have long noted these large flights (Sumichrast 1869, Chapman 1898, Loetscher 1941, 1955, Bussjaeger et al. 1967, Purdue et al. 1972). Although most of these reports primarily focus on raptors (Thiollay 1979, 1980, Tilly et al. 1989, Ruelas 1992, Ruelas et al. 2000), there is one report devoted to wading birds (Castillejos and Rodríguez 2002).

In this chapter I address two central questions about migration in central Veracruz: (1) What is the magnitude of the flights? and (2) What is the combination of geographic and atmospheric conditions that result in one such geographic bottleneck for migrants? To describe these flights and to determine how migrants respond to weather and geographic features, I list the species involved, quantify the magnitude of their

flights, determine the extent of annual variation of these migrations, and classify the flocking behavior and choice of assisted flight modes by species.

METHODS

The central region of the state of Veracruz, Mexico, lies at the intersection of two major mountainous systems, the Sierra Madre Oriental and the Central Volcanic Belt, which constrain the width of the Gulf Coastal Plain at about 19° N, ca. 30 km north of Veracruz City. The foothills of the Cofre de Perote volcano (4,250 m above the sea level, hereon mASL) continue east along the Sierra de Manuel Díaz, to reach the Gulf of Mexico at the vicinity of the fishing village of Villa Rica. This reduction in the course of the Gulf lowland coastal plain forms a geographic bottleneck that funnels spring and fall migrations (Ruelas et al. 2000, 2005).

I started this research with a general understanding of the magnitude and dynamics of migration in the region, based on published reports (especially Thiollay 1980 and Tilly et al. 1989) and my own preliminary observations carried out in the spring and fall 1989. I recorded this migration from a survey line of fixed localities along an east to west transect that roughly follows the course of Federal Highway 140 (circa 19°N). During the fall and spring migration seasons, between 2-5 count sites were used simultaneously, spaced at least 10 km from each other to avoid double-counting of migrants (Table 1).

During the first years of this study (1991-1993), my field teams and I covered more localities (n=4 or 5) that ranged from coastal to mountainous for less time (e.g. 61 days in 1991) to assess the width of the migration front. Based on my understanding of

the geographic distribution of migration, I implemented longer field seasons (93 days from 1995 to the present) at the two most active localities per field season.

At each observation site, three observers (two field biologists and one field assistant) recorded the migration from a vantage point (a hill, an observation tower, or a tall building) to allow a view of at least 270 degrees. The two main observers split the field of view in half and used 8 or 10x binoculars to scan the sky for migrants and a 20x Kowa TSN telescope mounted on a sturdy tripod to identify distant migrants. Observers alternated the section of the sky they covered every hour, actively searched for birds with naked eye and binoculars, and identified migrants using Dunne et al. (1989), Howell and Webb (1995), Sibley (2000) and Wheeler and Clark (2003).

I randomly assigned both field biologists and field assistants to teams and localities, and each field crew worked two days on and one off to distribute observer bias and reduce observer fatigue. My field teams and I directly counted the number of birds when flock sizes were low (e.g. <75 birds) and made estimations when numbers were large. Most birds occur in large flocks that use thermals for flight, and teams counted or estimated the number of migrants once the thermal-climbing period had finished and birds were in their straight-line gliding flights. 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. Most commonly used multiples in these estimations were 3, 5, 10, 20, and 50 individuals.

Flocks frequently contain multiple species, and we used separate tally counters for the three or four of the most common species in the flock. We verbally communicated to field assistants the sightings of species in low numbers. The primary function of field

assistants was to write down data, make sure field biologists were each focusing on separate streams of migrants, and to see that low flying birds did not pass unrecorded.

This protocol for data collection was followed seasonally during the course of all field observations. In order to ensure a high standard of quality in the data collected, field biologists had to complete at least two seasons of field experience before occupying these positions and I compiled detailed instructions for data collection in a written field manual.

I made fall migration counts from 20 August through 20 November and spring counts roughly from 20 February through 15 May (Table 1). From 0800-1800 CST, teams collected hourly weather (e.g. temperature, wind speed, and wind direction), flight-recording conditions (e.g. number of observers and visibility) and migrant count totals following a slightly modified protocol of the standardized procedure of the Hawk Migration Association of North America (Kerlinger 1989, HMANA 2005). I classified the observed behavior of migrants in three flocking categories, three types of flight mode, and presence/absence of water crossing behavior, although these behaviors were not quantified by species.

Because I observed most species using thermal convection, I assumed temperature, shear wind, and barometric pressure would not be good predictors of geographic distribution of migration if treated separately. In order to determine the availability of thermal convection for migrants, I calculated the Richardson's number (Ri) for each different counting station/elevation. Ri is based on a simple model that combines the adiabatic (vertical) distribution of these three variables at the lower and

upper limit of the atmospheric boundary layer. It produces a quantitative measure of turbulence or thermal convection (Arya 1988:75):

$$Ri = \frac{g}{T_v} \frac{\delta\Theta_v}{\delta z} \left| \frac{\delta V}{\delta z} \right|^{-2}$$

where g is the acceleration of gravity, T_v is the average temperature in °K (°C+273.15), $\delta\Theta_v$ the difference of temperature on the upper of the boundary layer minus surface temperature, δz the height of the boundary layer minus the altitude of the locality, and δV the difference in wind speed between the upper and lower limits of the boundary layer. I obtained daytime historic average data for height of boundary layer, temperature, and advection from the on-line clearinghouse of the Climate Diagnostic Center of the National Oceanic and Atmospheric Administration (CDC 2005) and from Tejada et al. (1989), to calculate the seasonal average per site.

To map the geographic distribution of migration in spring and fall, I superimposed the calculations made for different altitudes in both field seasons to a Geographic Information System (GIS) layout that encompasses the region around my study sites. This GIS layout is 1 degree of latitude by 1 degree of longitude, scale 1:250,000, and is based on a 100-m resolution digital elevation model commercially available (INEGI 2005) reclassified in six altitudinal intervals using ArcView Version 3.2 (ESRI 2000).

This analysis excludes Black Vultures (*Coragyps atratus*), several duck and geese species that (locally) exhibit mostly nocturnal migration habits, many of the smaller egrets and herons with unclear diurnal/nocturnal migration habits, accidental species (e.g. a single record of 5 Sandhill Cranes [*Grus canadensis*] on 21 September 2000), and other

infrequent species which await careful, detailed analysis and documentation (e.g. several records of Northern Goshawks [*Accipiter gentilis*] in the falls of 1996, 1997, and 2004). A more complete list of migrants is available in Ruelas et al. (2005).

RESULTS

Species present and the scale of their migration.- My field teams and I recorded the annual migration of 33 species of large, soaring, diurnal migrants from nine families. Species quantities varied from a few individuals to millions, and the scale (relative magnitude) of their migration was different in spring and fall. Spring migration was of lesser magnitude, with an average of over 800,000 migrants (maximum of 1,282,834 in spring 2004). I recorded much larger flights during the fall (average of more than 5.1 million birds, maximum of 6,797,711 birds in fall 2002) (Table 2).

In spring, migrations were dominated by seven species ($>10^3$ individuals): American White Pelican, Anhinga, Turkey Vulture, Mississippi Kite, Broad-winged Hawk, Swainson's Hawk, and American Kestrel (scientific names in Table 2). These comprised 85.7% of the total number of individuals recorded. The late spring passage of the Wood Stork through the region continues through the month of May and June of each year, although we have never extended our observations past 15 May. Wading birds were less abundant in spring counts because longer-term count sites selected are further inland than fall sites.

Excluding the American Kestrel and including the Wood Stork, the dominant species in the fall are the same as spring. These birds were recorded in large numbers ($>10^5$ individuals) and comprise 60.3% of the migration. Many migrants were recorded

as unidentified (\bar{x} =0.02% in spring, and \bar{x} =1.96% in the fall) of which nearly three-quarters are buteos.

The number of migrants recorded annually varies (Table 2). As expected, the average coefficient of variation is high, 65% for the spring and 88% in the fall, although this may be an artifact of the larger seasonal coverage of the fall season. The inter-annual variation observed in migration counts is larger for the species that migrate in lower numbers, while more abundant species exhibit lower fluctuations. The spring season seems to be overall more variable than fall, and the fall's narrower distribution of residuals is more closely fitted to the negative trend line (Fig. 1).

Flocking tendencies and flight mode.- Most species (n=27) form flocks during migration, with 13 species (39%) forming single-species flocks, and 16 species (48%) forming multi-species flocks (Table 2). Although 20 species (60%) were recorded as solitary, there are only six species we consider strict solitary migrants (White-tailed Kite, Bald Eagle, Northern Harrier, Red-tailed Hawk, Ferruginous Hawk, Golden Eagle, and Merlin), including several for which solitary migration habits are a consequence of their rarity (e.g. Bald and Golden Eagles) (the breakdown of categories does not add up to 100% because there are overlaps, Table 2).

Use of thermal convection is clearly a dominant flight strategy, more commonly observed among most of the species than alternative use of shear wind or powered flight. All the species use thermal convection, 23 species (69%) use powered, unassisted flight, and six species (18%) use shear winds (shear wind is the difference in wind speed and/or direction between two points in the atmosphere and can be either vertical or horizontal). No species was observed strictly using powered flight. Thermal-riding species follow the

same basic cross-country flight technique described by Pennycuik (1972, 1998): flocking migrants locate thermals, climb to the highest altitude possible turning tight circles close to the center of the thermal, and then glide (sink) in their desired flight direction. The process repeats itself when then low-flying birds find the stronger lift on the lower section of the following thermal and climb again.

In locations or conditions of poor thermal convection, colonial wading birds (pelicans to ibises in Table 2) continue their flights mostly in single-species flocks using shear wind as an alternative. In most raptors, the alternative is to move towards solitary flights. Long-distance, abundant species of flocking birds that favor thermal convection such as Broad-winged Hawk, Swainson's Hawk, and Turkey Vulture, may not migrate in the absence of thermal convection. Powered flight is a widespread, but less frequently used, locomotion strategy.

Water crossing behavior.- We regularly recorded individuals of only seven (21%) species flying over the Gulf of Mexico. This behavior was not quantified per species, and migrants were detected mostly within ~500 m of shoreline, although I do not exclude the possibility that some wading birds might migrate further from the coast.

Thermal convection and migration.- In spring, thermal convection was higher than in the fall (spring mean $Ri=0.16$). Its distribution follows a hyperbolic curve, with coastal sites subject to high variation; and, more uniform, lower Ri values (higher thermal convection) in the middle sections of the coastal plain (Fig 2). At inland elevations higher than 800 mASL, thermal convection values increase sharply (Fig. 2). The rate of migrants recorded per hour was negatively correlated to Ri values: coastal counts and the most

inland site are lower than the ones obtained at the middle section of the coastal plain ($r=-0.99$, $n=6$, $P<0.001$).

The distribution of thermal convection in the fall is lower than in spring (mean $Ri=0.35$; $t=2.76$, $df=4$, $P=0.02$) and followed a less clear pattern. Locations at lower elevations have a seasonal variation of similar mean values and relatively narrow standard deviations, with a slight increase towards 400 mASL elevation. Ri values have a sharp increase in inland locations above 800 mASL, with values below the 'threshold' of thermal convection suggested by Arya (1988). The rate of migrants per hour was high in localities <200 mASL and decreases rapidly at inland, higher elevations, and it was also negatively correlated with Ri values ($r=-0.88$, $n=6$, $P<0.001$). The rate of migrants per hour in localities >400 mASL is 3-4 orders of magnitude lower than locations in the coastal plain, which means migrants are largely restricted to elevations below Rinconada, (400 mASL) a locality within <30 km from the coast (Fig. 2).

DISCUSSION

Each spring and fall, millions of diurnal, large, soaring migrants funnel through a geographic bottleneck in central Veracruz, Mexico. Birds that largely avoid crossing over water typically aggregate in flocks that use thermal convection available in the coastal plain lowlands as their favored mean of assisted flight. Here I address the two primary goals for this chapter, and make a statement on applications and significance of my results.

Magnitude of migrations and a comparison with other important migration sites.- My research places central Veracruz among the most important locations for migratory

wading birds, vultures, and raptors in the world (Ruelas et al. 2000, Zalles and Bildstein 2000). In the few years since the publication of Zalles and Bildstein's directory (2000), researchers from Costa Rica (Porrás-Peñaranda et al. 2004) and Panama (Batista et al. 2005) have presented new evidence to further document important sites for migration along Mesoamerica, the most important corridor for migratory raptors in the Americas (Bildstein and Zalles 2001).

Zalles and Bildstein (2000) have identified other geographic bottlenecks for raptor migration in the world. Perhaps the most important outside the Americas is the corridor along the east end of the Mediterranean, where migrants from Eurasia funnel into Africa over Syria, Lebanon, Jordan, Palestine, and Israel (Moreau 1953, Safriel 1968, Christensen et al. 1981); this route is also used by pelicans and storks (Leshem and Yom-Tov 1996) (Table 3).

The potentials for population monitoring have helped in the development of raptor migration studies. Migration counts of raptors and vultures have been used as a monitoring tool (Hussell 1981, Bednarz et al 1990, Hoffman and Smith 2003) and studies based on these counts are relatively widespread (Kerlinger 1989). Information on migrant wading birds, however, is scarce, because counts are not a methodology commonly used to study their populations (Frederick et al. 1996, Morss 2001). Rather, monitoring techniques such as aerial surveys and colony counts are the basis of demographic studies (Coulter et al. 1999, Knopf 2004).

Why are fall counts from Veracruz nearly four times the magnitude of spring flights? I believe there are two main factors: (1) A more widespread spring migration front that is tracked from sites too far from each other (~20 km apart), increases the

potential area where migrants pass unrecorded; and (2) The higher average thermal convection of the spring season (which locally corresponds to the dry season), results in poor visibility conditions (bright, hazy skies) and a possibly higher migration height. Fall flights are restricted to a much narrower geographic area, with overall better conditions for recording migration (lower temperatures, comparatively less hazy skies, and reduced observer fatigue in what locally corresponds to the rainy season). Lower thermal convection that may result in migrants being easier to detect flying at lower heights.

How accurate are these counts and estimations? I have explored this issue to some extent, through experiments using slides, video, and software (ERI unpublished data). My inconclusive results show that a larger magnitude of flight increases estimation errors in all cases and I conservatively believe my counts and estimations are at least a consistent measure of the migration observed. The magnitude of flights in species recorded in large numbers, including the seven species occurring at scales $>10^5$ in the fall, have an average coefficient of variation of 35.7%.

Locomotion, flocking behavior, and the distribution of migration.- Central Veracruz concentrates the conditions for the two most common types of assisted flight, appropriate thermal convection for pelican, stork, vulture, and raptor species, and constant wind shear for coastal wading birds, in a relatively small area. Thermal-riding is preferred to other alternative flight strategies possibly because it is energetically cheaper than wind shear and the several forms of orographic lift utilized in more northern localities, where thermal convection is poor or a more temporally-unstable atmospheric condition (Haugh 1974, Hederström 1993, Spaar 1997, Brandes and Ombalski 2004).

My observations support previous hypotheses which state that flocking is a behavior that increases migration efficiency under different types of atmospheric conditions (Shamoun-Baranes et al. 2003). Tucker (1971) demonstrated that flocking and ‘V’ formations in wading bird species represent significant savings in energetic expenditure, whereas Kerlinger (1985) hypothesized that the function of flocking in long distance migrants is a means for locating irregularly distributed thermal convection.

Central Veracruz, a geographic bottleneck for migration.- A combination of several features results in a bottleneck of global importance for migration of large, diurnal soaring birds. Mesoamerica (Mexico through Panama) is the only available, relatively narrow, bridge of land between North and South America. For 22 species, central Veracruz is located near the southern end of their breeding range (lower third) and near the northern end (upper third) of the wintering range, and these may be considered partial migrants (Appendix 1). For three species of total migrants (Mississippi Kite, Broad-winged Hawk, and Swainson’s Hawk), my study site is located between breeding and winter ranges, and it is possible that most of their global population migrate along this route (Goodrich et al. 1996, England et al. 1997, Parker 1999).

This geographic location maximizes the total number of migrants potentially using this migration corridor. The distribution of spring and fall migration in central Veracruz is restricted to the lower elevations and foothills of the Sierra Madre Oriental, where migrants follow a wide-front migration pattern that does not stick to ‘leading lines’ (as conceptualized by Mueller and Berger 1967), but is funneled through ‘diversion lines’ (fide Farmer et al. unpublished manuscript), a well-known characteristic of large, soaring, diurnal migrant birds (Kerlinger 1989, Leshem and Yom-Tov 1998).

The Gulf of Mexico limits the east edge of the migration front of most of the species (Kerlinger 1985). The otherwise-wide Gulf coastal plain is bordered at its west end by the Sierra Madre Oriental, a mountain range that commonly reaches altitudes >2,000 mASL. The distribution of thermal convection is a more plastic constraint for migration than the Gulf, but birds rarely exceed altitudes of 400 mASL in the fall and 1,600 mASL in spring. Although I have not collected data at elevations >1,600 mASL (Xalapa), I expect migration to follow this distributional trend and be largely limited to elevations lower than 1,600 mASL. There may be exceptional occasions in which higher than normal thermal convection availability may enable birds to migrate at higher altitudes.

The significance of this research lies in the applications of information on stopover ecology of migrants (Chapter 2), to habitat conservation (Appendix 1, Duncan et al. 2002), and the potential monitoring applications for some species (Chapter 4), which could extend its scope to a continental, global population scale.

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Table 1. Localities for the study of vulture, raptor, and wading bird migration in Veracruz, Mexico. Count sites in use, elevation in meters above the sea level (mASL), and distance from the Gulf of Mexico shoreline.

Locality	Elevation (mASL)	Distance (W) from the coast in kilometers	Season/year in use
Xalapa 19°32'N-96°55'W	1,440	61.25	Spring 1991, 1994 Fall 1992
Miradores 19°28'N- 96°47'W	925	46.56	Fall 1992
Cerro Gordo 19°26'N- 96°42'W	660	38.75	Spring 1991, 1994, 2004 Fall 1992
Rinconada 19°21'N- 96°34'W	313	26.25	Spring 1991, 1994, 2004 Fall 1993
Río Escondido 19°20'N- 96°32'W	160	25.01	Spring 1991, Fall 1992
Chichicaxtle 19°21'N- 96°28'W	120	17	Spring 1995 Fall 1992-1993, 1995-2004
Cardel 19°22'N- 96°22'W	29	7	Spring 1994 Fall 1992-2004
La Antigua 19°17'N- 96°17'W	10	1	Spring 1991
Chachalacas 19°25'N- 96°19'W	10	0.50	Fall 1992

Table 2. Magnitude of wading bird (Pelecaniformes: Pelecanidae, Phalacrocoracidae, Anhingidae; Ciconiiformes: Ardeidae, Threskiornithidae, Ciconiidae), New World vulture (Ciconiiformes: Cathartidae), and raptor (Falconiformes: Accipitridae, Falconidae) migration recorded in spring and fall in Veracruz, Mexico.

Flocking tendencies (2a) are classified as S=solitary, SS=single-species flock, MS=multispecies flock; Flight mode categories are TC=thermal convection, WS=wind shear, and PF=powered flight; Kerlinger (1989:123) coined the term "thermal obligates" for species that exclusively use thermal convection.

Spring data (2b) were collected in 1991, 1994, 1995, and 2004 (n=4 field seasons), but only 1994 and 2004 data (8 March-8 May) are used in the comparisons, due to differences in localities and duration of field seasons.

Fall data (2c) were collected from 1992-2004 (n=13 field seasons, 20 August-20 November), but data from 1992-1994, and 1997 are excluded from the analysis due to differences in localities and duration of field seasons.

(2a)

Species		Flocking tendency	Flight mode	Water crossing
Family Pelecanidae				
American White Pelican	<i>Pelecanus erythrorhynchos</i>	SS	TC, WS, PF	Yes
Family Phalacrocoracidae				
Neotropic Cormorant	<i>Phalacrocorax brasilianus</i>	SS	WS, PF, TC	Yes
Double-crested Cormorant	<i>Phalacrocorax auritus</i>	SS	WS, PF, TC	Yes
Unidentified Cormorant	<i>Phalacrocorax</i> sp.			
Family Anhingidae				
Anhinga	<i>Anhinga anhinga</i>	SS, MS	TC	No
Family Ardeidae				
Great Blue Heron	<i>Ardea herodias</i>	S, SS	PF, TC, WS	Yes
Family Threskiornithidae				
White Ibis	<i>Eudocimus albus</i>	SS	PF, WS, TC	Yes
White-faced Ibis	<i>Plegadis chihi</i>	SS	PF, WS, TC	Yes

Family Ciconiidae

Jabiru	<i>Jabiru mycteria</i>	S, SS	TC	No
Wood Stork	<i>Mycteria americana</i>	SS, MS	TC	No

Family Cathartidae

Turkey Vulture	<i>Cathartes aura</i>	S, MS	TC	No
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Family Accipitridae

Osprey	<i>Pandion haliaetus</i>	S, MS	TC, PF	No
Hook-billed Kite	<i>Chondrohierax uncinatus</i>	S, SS	TC, PF	No
Swallow-tailed Kite	<i>Elanoides forficatus</i>	S, MS	TC, PF	No
White-tailed Kite	<i>Elanus leucurus</i>	S	TC, PF	No
Mississippi Kite	<i>Ictinia mississippiensis</i>	S, MS	TC, PF	No
Plumbeous Kite	<i>Ictinia plumbea</i>	MS	TC, PF	No
Bald Eagle	<i>Haliaetus leucocephalus</i>	S	TC	No
Northern Harrier	<i>Circus cyaneus</i>	S	TC, PF	No
Sharp-shinned Hawk	<i>Accipiter striatus</i>	S, MS	TC, PF	No
Cooper's Hawk	<i>Accipiter cooperii</i>	S, MS	TC, PF	No
Gray Hawk	<i>Asturina nitida</i>	S, MS	TC, PF	No
Common Black Hawk	<i>Buteogallus anthracinus</i>	S, MS	TC, PF	No
Harris's Hawk	<i>Parabuteo unicinctus</i>	S, MS	TC, PF	No
Red-shouldered Hawk	<i>Buteo lineatus</i>	S, MS	TC	No
Broad-winged Hawk	<i>Buteo platypterus</i>	MS	TC	No
Swainson's Hawk	<i>Buteo swainsoni</i>	MS	TC	No
Zone-tailed Hawk	<i>Buteo albonotatus</i>	MS	TC	No
Red-tailed Hawk	<i>Buteo jamaicensis</i>	S	TC, PF	No
Ferruginous Hawk	<i>Buteo regalis</i>	S	TC, PF	No
Golden Eagle	<i>Aquila chrysaetos</i>	S	TC	No

Family Falconidae

American Kestrel	<i>Falco sparverius</i>	S, SS, MS	TC, PF	No
Merlin	<i>Falco columbarius</i>	S	PF, TC	No
Peregrine Falcon	<i>Falco peregrinus</i>	S, MS	PF, TC	No

(2b)

Spring (1994-2004)					
	Mean	Range		SD	CV
Family Pelecanidae					
American White Pelican	1,619.0	1,179	2,059	622.25	38.43
Family Phalacrocoracidae					
Neotropic Cormorant	1.0	1	1	0.00	0.00
Double-crested Cormorant	0.0	0	0	0.00	0.00
Unidentified Cormorant	0.0	0	0	0.00	0.00
Family Anhingidae					
Anhinga	3,103.5	1,319	4,888	2,523.66	81.32
Family Ardeidae					
Great Blue Heron	0.5	0	1	0.71	141.42
Family Threskiornithidae					
White Ibis	3.0	1	5	2.83	94.28
White-faced Ibis	70.5	0	141	99.70	141.42
Family Ciconiidae					
Jabiru	0.0	0	0	0.00	0.00
Wood Stork	170.5	2	339	238.29	139.76
Family Cathartidae					
Turkey Vulture	277,455.0	156,626	398,284	170,878.01	61.59
Family Accipitridae					
Osprey	602.0	476	728	178.19	29.60
Hook-billed Kite	58.5	52	65	9.19	15.71
Swallow-tailed Kite	8.0	3	13	7.07	88.39
White-tailed Kite	0.0	0	0	0.00	0.00
Mississippi Kite	21,062.0	11,701	30,423	13,238.45	62.85
Plumbeous Kite ¹	0.3	0	0	0.00	0.00
Bald Eagle	0.5	0	1	0.71	141.42
Northern Harrier	69.0	40	98	41.01	59.44
Sharp-shinned Hawk	598.0	520	676	110.31	18.45
Cooper's Hawk	552.0	525	579	38.18	6.92
Gray Hawk	38.5	0	77	54.45	141.42
Common Black Hawk	0.3	0	1	0.50	200.00
Harris's Hawk	2.0	1	3	1.41	70.71
Red-shouldered Hawk	19.0	4	76	15.64	82.33

Broad-winged Hawk	319,094.8	80,004	1,276,379	211,890.72	66.40
Swainson's Hawk	105,403.3	14,783	421,613	75,607.00	71.73
Zone-tailed Hawk	22.0	9	35	18.38	83.57
Red-tailed Hawk	44.5	25	64	27.58	61.97
Ferruginous Hawk	0.0	0	0	0.00	0.00
Golden Eagle	2.0	1	3	1.41	70.71
Unidentified Kite	0.0	0	0	0.00	0.00
Unidentified Accipiter Hawk	40.0	37	43	4.24	10.61
Unidentified Buteo Hawk	3,574.5	247	6,902	4,705.80	131.65
Family Falconidae					
American Kestrel	1,004.0	822	1,186	257.39	25.64
Merlin	27.5	8	47	27.58	100.28
Peregrine Falcon	97.5	61	134	51.62	52.94
Unidentified Falcon	8.0	0	16	11.31	141.42
Spring season summary	812,047.0	435,233	1,188,861	532,895.47	65.62

(2c)

	Fall (1995-2004)				
	Mean	Range	SD	CV	
Family Pelecanidae					
American White Pelican	85,679.0	54,507	128,757	32,476.35	37.90
Family Phalacrocoracidae					
Neotropic Cormorant	96.7	29	205	94.79	98.05
Double-crested Cormorant	42.0	4	95	47.32	112.66
Unidentified Cormorant	0.7	0	2	1.15	173.21
Family Anhingidae					
Anhinga	31,633.5	18,837	41,440	9,011.62	28.49
Family Ardeidae					
Great Blue Heron	541.0	17	2,167	805.51	148.89
Family Threskiornithidae					
White Ibis	1,469.3	230	4,693	1,690.72	115.07
White-faced Ibis	1,985.8	499	3,871	1,372.62	69.12
Family Ciconiidae					
Jabiru	4.4	0	21	9.29	211.13
Wood Stork	56,975.5	24,915	121,791	33,205.34	58.28
Family Cathartidae					
Turkey Vulture	1,895,679.7	1,474,797	2,677,355	387,839.48	20.46
Family Accipitridae					
Osprey	3,040.8	1,147	5,072	1,085.34	35.69
Hook-billed Kite	175.6	84	300	77.16	43.95
Swallow-tailed Kite	162.9	90	286	75.25	46.20
White-tailed Kite	0.7	0	2	1.00	150.00
Mississippi Kite	157,199.4	32,568	306,274	87,640.11	55.75
Plumbeous Kite	4.1	0	17	6.11	148.68
Bald Eagle	0.1	0	1	0.33	300.00
Northern Harrier	447.9	106	850	280.22	62.56
Sharp-shinned Hawk	4,280.9	2,173	10,462	2,600.61	60.75
Cooper's Hawk	2,433.9	932	4,019	1,046.83	43.01
Gray Hawk	180.3	0	612	256.26	142.10
Common Black Hawk	2.1	0	10	3.76	177.94
Harris's Hawk	6.9	0	12	3.72	54.04
Red-shouldered Hawk	10.1	1	27	7.47	73.92

Broad-winged Hawk	1,931,255.6	1,534,556	2,389,232	287,822.28	14.90
Swainson's Hawk	812,419.8	388,916	1,197,850	280,788.52	34.56
Zone-tailed Hawk	117.4	31	173	47.14	40.14
Red-tailed Hawk	197.0	100	352	85.92	43.61
Ferruginous Hawk	0.6	0	2	0.73	130.77
Golden Eagle	0.8	0	3	1.30	167.36
Unidentified Kite	0.7	0	6	2.00	300.00
Unidentified Accipiter Hawk	181.1	24	810	248.61	137.27
Unidentified Buteo Hawk	77,933.3	1,220	256,771	88,095.96	113.04
Family Falconidae					
American Kestrel	7,507.3	2,935	21,642	6,488.92	86.43
Merlin	157.0	44	383	102.54	65.31
Peregrine Falcon	748.3	205	1,469	338.44	45.23
Unidentified Falcon	32.3	0	90	32.60	100.81
Fall season summary	5,113,415.6	4,077,152	6,797,711	1,923,725.72	37.62

¹Under field conditions in Veracruz, there are notorious difficulties to positively identify Plumbeous Kites from the closely-related Mississippi Kites. Although very low quantities of them are recorded every season, it is possible that more of them are included as unidentified. Due to the close proximity of my research sites to the northern limit of their breeding range, I expect this number to be low.

Table 3. Maximum number of birds recorded at migration bottlenecks of global importance.

Locality	Wading birds ¹	New World Vultures	Raptors	Notes
Veracruz, Mexico	128,757 pelicans 121,791 storks	2,677,355	4,120,356	Records for 33 species tallied from two localities between 1991-2004 (this study)
Talamanca, Costa Rica	n/a	1,367,200	1,611,902	Records of 17 species tallied from two localities in falls of 2000-2001, Porrás-Peñaranda et al. (2004)
Isthmus of Panama	n/a	1,399,847	1,725,639	Records of 15 species tallied from a survey line of nine sites in fall of 2004 (Batista et al. 2005)
Israel	301,048 pelicans 76,909 storks	n/a	1,193,751	Records for 35 species tallied from a survey line of max. 20 sites between 1977-1990 (Leshem and Yom-Tov (1996)

¹Only includes counts of pelicans and storks. In Veracruz, records pertain to American White Pelican and Wood Stork; In Israel, records pertain to White Pelican (*Pelecanus onocronatus*) and White Stork (*Ciconia ciconia*).

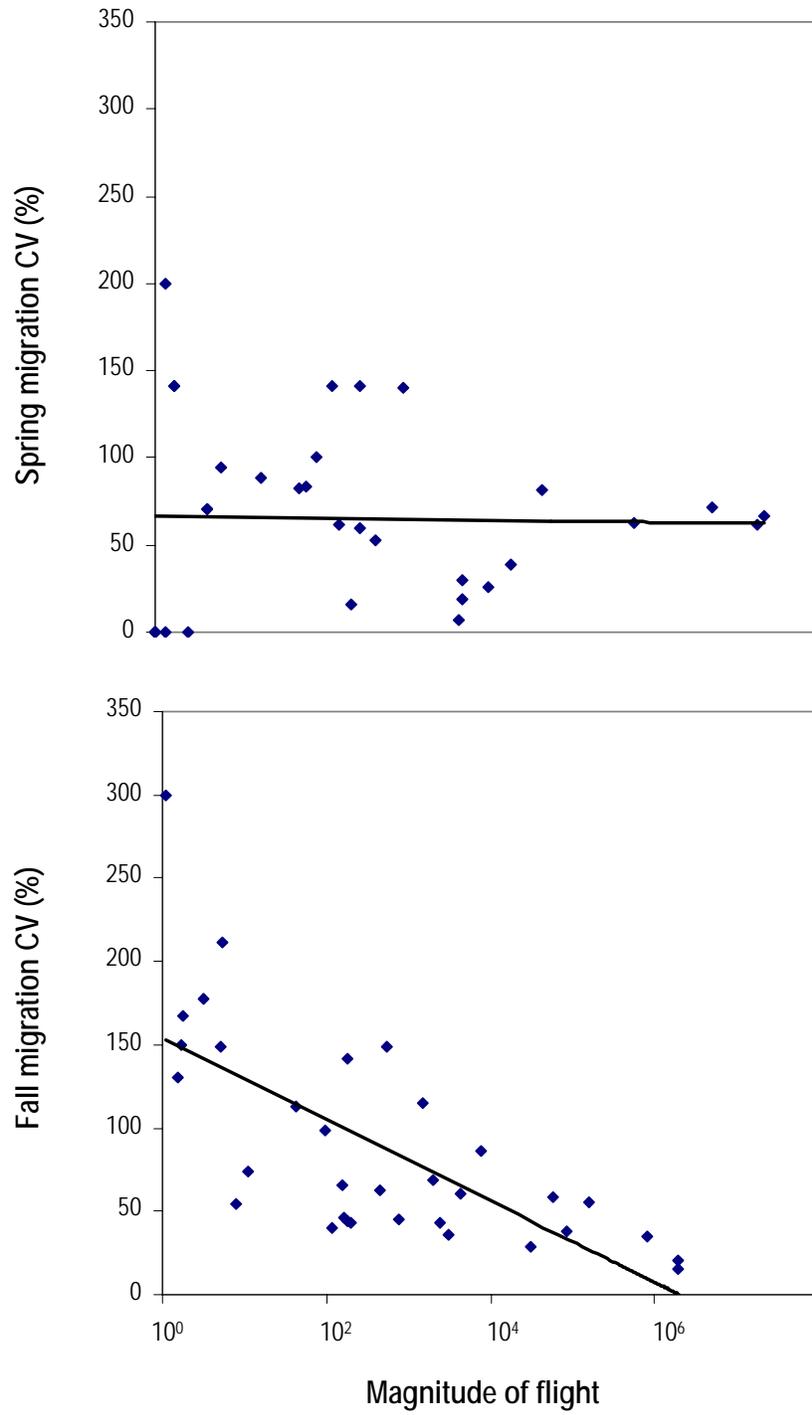
FIGURE LEGENDS

Figure 1. Mean annual variation in the counts of migrating wading birds, vultures, and raptors in spring and fall, 1994-2004. Species with migrations of lesser magnitude exhibit larger inter-annual fluctuations in the number recorded. Spring migrations have higher inter-annual variation than fall.

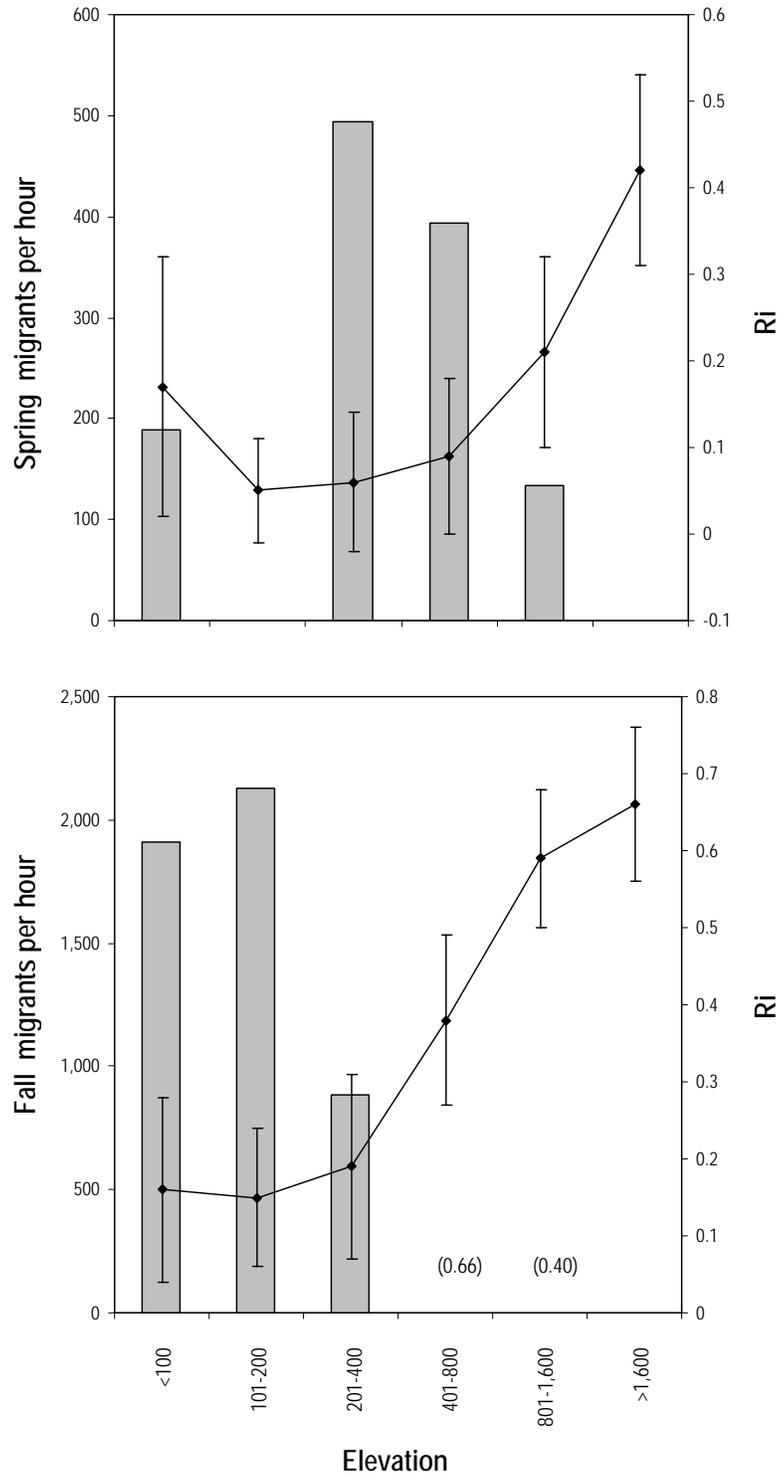
Figure 2. Rate of passage of wading birds, vultures, and raptors (mean number of migrants per hour, all species, gray bars for axis y1) and the distribution of thermal convection (black lines for axis y2) at different elevations in central Veracruz, Mexico. The rates of passage for spring include observations made during a 61-day period between 1 March-30 April 1991, and fall data collected during the 93-day period between 20-August-20 November 1992. The measure of thermal convection is given by the Richardson's number ($Ri \pm SD$), where high Ri values mean low convection.

Figure 3. Location of central Veracruz, Mexico (A), and the altitudinal distribution of thermal convection and rates of passage of migrant wading birds, vultures, and raptors (B).

(Fig. 1)



(Fig. 2)



CHAPTER 2

TEMPORAL DYNAMICS OF NEW WORLD VULTURE AND RAPTOR MIGRATION THROUGH VERACRUZ, MEXICO

Abstract.- Understanding and quantifying the patterns of bird migration over space and time has been a useful means to gain insights into many aspects of its migration ecology and in designing long-term monitoring protocols.

My objectives in this paper are (a) To present a quantitative description of the temporal dynamics of an assemblage of one species of vulture and 11 species of diurnal raptors, (b) To use these measures of intra- and inter-annual variation to make some inferences about the effects of variables at multiple scales in species' migration patterns, and (c) To evaluate the implications of these temporal variations on long-term monitoring schemes.

I studied the temporal dynamics of this assemblage of species during the course of three spring and ten fall seasons (1991-2004). My observations were collected in Veracruz, Mexico, a location where a geographic bottleneck funnels millions of migrant vultures and raptors during spring and fall.

The patterns I present are a species-by-species description of spring and fall migration, and a characterization and quantification of the patterns for the complete assemblage using Detrended Correspondence Analysis (DCA). I made multiple within-

and among-year comparisons to test the consistence of these patterns over time. During spring, migration is unimodal in seven species and has a bimodal/unclear distribution pattern for five species. Duration of species' migration through the region lasted between 43 and 70 days (mean=53 days). The migration season of four species is significantly shorter in spring than in the fall. I found significant differences in timing of migration across years for all species, with peak dates differing between 3-11 days. In fall, migration is unimodal for ten species. Mean duration of fall migration recorded ranges between 20-74 days (mean=52 days). The duration of fall migration was significantly shorter than spring for five species. With no exceptions, all species had significant differences in timing of migration across years, with peaks differing between 4-9 days.

Analyses of spring data using DCA show no discernible pattern because data does not meet DCA model assumptions. In the fall, the pattern has the stair-step shape of assemblages with clumped temporal distributions. Fall assemblage patterns are not significantly different among years. I conclude that a careful analysis of single-species vs. species-assemblage patterns can help us to make a qualitative distinction between local vs. range-wide variables in migration patterns and direct the design of long-term monitoring seasonal coverage.

Key words: Dynamics, raptors, vultures, migration, seasonal timing, Detrended

Correspondence Analysis.

INTRODUCTION

One of the most common products of vulture and raptor migration studies is the description of the temporal distribution of its passage over a locality (Devereux et al. 1985, Kerlinger 1989, Harmata et al. 2000). These temporal patterns provide basic information about the statistical properties of its distribution, and have been commonly used: (1) To quantify the effects of weather variables on migration (Kerlinger and Gauthreaux 1985); (2) To make inferences on the biogeography and ecology of the species involved (Shamoun-Baranes 2003); (3) To assist in the estimation of global population size, particularly for species whose total population might potentially pass through the site (Appendix 1, Leshem and Yom-Tov 1996); and (4) To plan the optimal seasonal coverage for long-term monitoring (e.g. Bednarz et al. 1990, but see Kerlinger 1989:31-34 for a discussion of its limitations). The seasonal timing of migration is assumed to be a relatively stable feature, with fluctuations commonly documented within a migration season rather than across multiple years (Haugh and Cade 1966, Mueller and Berger 1967, Alerstam 1978, 1990, Titus and Mosher 1982, Allen et al. 1996, Berthold 2001).

The historic individual-species focus of these analyses has recently been expanded by developments in understanding and quantifying patterns of assemblages of multiple species (Rotenberry and Chandler 1999, Deppe and Rotenberry 2005). The analysis of migration patterns of a set of species arises from the perspective that species turnover can be viewed as a dynamic, phenological process where species sequentially replace others over time at migration sites.

This recent approach has been made through the application of an ordination technique called Reciprocal Averaging or Detrended Correspondence Analysis (herein DCA, Hill and Gauch 1980), a multivariate model commonly utilized in community analysis (Pielou 1984). Such an approach allows the researcher to understand the relationships between multiple species and to quantify the observed rhythm of passage in ‘waves’ (Rotenberry and Chandler 1999). The patterns observed in a species (or an assemblage) are the result of variables of different scale that modify these patterns. Examples of these variables include wind speed, wind direction, frequency and duration of fronts, distance between breeding and wintering ranges, range size, age, and possibly diet (Newton 1979, Leshem and Yom-Tov 1996, Allen et al. 1996, DeLong and Hoffman 1999, Shamoun-Baranes et al. 2003, Thorup et al. 2003). My hypothesis is that these variables operate at different points of a scale-dependent process, whose effects can be discriminated through the analysis of dynamics of individual species versus species-assemblage (Titus and Mosher 1982, Ketterson and Nolan 1983, 1985).

This paper has three main objectives. The first is to provide a quantitative description of the temporal dynamics of the migration of an assemblage of one species of New World vulture and 11 species of diurnal raptors through central Veracruz, Mexico. Specifically, I present the seasonal timing of spring and fall migration for each species, and statistically compare the properties of each species’ passage across multiple years. I also quantify the phenological sequence and rhythm of passage of the complete assemblage of species and compare this sequence among years, as well as between spring and fall migration seasons.

My second objective is to use these measures of within and between annual variations to discuss the correspondence between variables of different scale with the phenology of migration.

The last objective is to discuss the implications of annual changes in the temporal dynamics of migration in the design of long-term monitoring schemes.

METHODS

Site description and field methods.- The central region of the state of Veracruz, Mexico, lies at the intersection of two major mountainous systems, the Sierra Madre Oriental and the Central Volcanic Belt, which constrain the width of the Gulf Coastal Plain to a narrow corridor of a few tens of kilometers at about 19° N, ca. 30 km north of Veracruz City. The foothills of the Cofre de Perote volcano (elevation 4,250 m above the sea level, hereon mASL) continue east along the Sierra de Manuel Díaz, to reach the Gulf of Mexico at the vicinity of the fishing village of Villa Rica. This reduction in the course of the Gulf lowland coastal plain forms a geographic bottleneck that funnels spring and fall migrations (Ruelas et al. 2000, 2005).

Teams of three observers atop vantage points distributed along a west to east survey line, perpendicular to the migration front, identified and recorded the number of migrant vultures and raptors. Field sites were located between 11-21 kilometers apart to avoid double counts of birds. Observers also collected data on the conditions for observation of migration and weather variables, using the standard data collection protocol of the Hawk Migration Association of North America (Kerlinger 1989; HMANA 2006).

In this description of seasonal timing, I combined data from two migration count sites per field season. During spring, our field teams made migration counts from Cerro Gordo and Rinconada, located 21 km of linear distance from each other. During fall, I made counts from Chichicaxtle and Cardel, located 11 km apart. The detailed description of the data collection protocol in use, location of counts sites to prevent double counts of migrants, optic and weather recording equipment, the rotation system used to distribute observer error, and the daily coverage of count sites, is available elsewhere (ms in prep.)

Data analysis.- In this analysis, I include spring data (n=3 field seasons) collected over a 37-86 day period between Julian days 51-135 (20 Feb -15 May) of 1991, 1994, and 2004. For an analysis of fall data (n=10 field seasons), I include data collected over a 93-day period between Julian days 232-324 (20 August-20 November) of 1993, 1995, 1996, and 1998-2004 (for a detailed description of these locations and field coverage per field season see Chapter 1 and Ruelas et al. 2005). I selected these dates and localities for analysis because they have the longest comparable coverage per field season and these are also the localities with the largest number of migrants recorded, at the peak of the geographic distribution of migration (ms. in prep.)

The fall data set is noticeably more robust than the spring data set because it covers a longer time series. In order to obtain a more complete characterization of the species' seasonal timing, the description of the seasonal timing for the spring of 2004 is based on an 86-day period between Julian days 51-135 (20 February-15 May), although inter-annual comparisons are based on a shorter, 37-day period, between days 75-111 (16 March – 21 April) for years 1991 and 1995.

To describe and quantify the statistical properties of the seasonal timing of each species per season, I used the PROC UNIVARIATE program of SAS (version 9.1, SAS Institute 2004). For each species, I provide (a) The average number of individuals recorded per season (with data from Chapter 1); (b) The duration (in days) of 95% of their migration (the difference between the upper and the lower 95% quantile dates); and (c) Comparisons of the quantity and distribution of migration in each species among different years using a Type I Analysis of Variance (PROC ANOVA of SAS) or Kuskal-Wallis tests for non-normal distributions.

Larger time series of fall data available (n=10 field seasons) allowed me do inter-annual orthogonal comparisons on each species to determine differences in seasonal distribution among field seasons and to group seasons that have similar timing. These orthogonal comparisons generate groupings of similar seasons where a larger number of groupings mean more inter-annual differences. These are expressed in SAS output as ‘t Groupings’ and are reported in the results section under each species.

Migration count data tend to be highly skewed, with a few days having large numbers of birds recorded and many days having only a few individual birds recorded (Dunn 2005). The seasonal timing figures are made by standardizing the total number of birds recorded and grouped in periods of five days to reduce the high variation observed in daily, raw data (Fig. 1).

In the analysis of temporal changes in the assemblage of species, I used DCA, a technique commonly utilized to characterize species turnover in communities over environmental gradients (Hill 1973, Hill and Gauch 1980, Pielou 1984). DCA has been used to model migration patterns of sets of multiple passerine species, using time as the

independent variable (Rotenberry and Chandler 1999). Under the DCA model, species turnover is viewed as a phenological process and is used to characterize the structure of data from an assemblage of multiple species. Species appear, increase in abundance, reach a peak, decrease, and disappear over a gradient, in this case a time period. Species sequentially replace others in this time gradient, and a difference of 4 units on DCA scores indicates complete species turnover. For a complete description of the rationale of DCA in migration pattern analyses, see Rotenberry and Chandler (1999) and Deppe and Rotenberry (2005).

One key assumption of DCA is that species have a normal (unimodal) temporal distribution. The characterizations obtained distinguish two types of patterns: (1) A straight-line pattern for assemblages with uniformly-spaced passage times among species, or (2) A stair-step pattern for assemblages of species with clumped/aggregated passage times. DCA produces a quantitative measure, an eigenvalue (λ), which is a correlation between species and count scores with a maximum value of 1. All DCAs were done using PC-ORD version 4.0 (McCune and Mefford 1999).

Because there are significant differences in the migration timing of species among different years, I made a separate DCA for each season. To determine differences in inter-annual migration patterns characterized by DCA species scores, I used ANCOVAs using day of the year as the covariate. To meet the ANCOVA model assumptions (normality and homogeneity of variance), I transformed the DCA scores through a Box-Cox transformation. However, I present these results in a scatter plot of untransformed scores in DCA axis 1 versus count date (in Julian days, maximum score value 4=complete species turnover) in order to visually compare the seasonal and annual

patterns observed among years and the influence of magnitude of migration in these patterns.

RESULTS

Seasonal timing of species.- The seasonal timing of spring and fall migration of one species of New World vulture and 11 species of diurnal raptors in central Veracruz, Mexico, is described below and illustrated in Figure 1. Here I provide the average number of individuals observed in spring and fall per 5-day period, describe the seasonal timing per season, identify the peak dates of migration, and provide information on differences and similarities among seasons.

Turkey Vulture (*Cathartes aura*). During spring migration (mean $n=277,455$ individuals), the Turkey Vulture is the earliest among dominant species. The early part of this migration period is truncated by survey dates (counts started when migration of this species was underway, and spring counts should start on Julian day 41 [10 February] to allow a more complete coverage). Ninety-five percent of the individuals are recorded between Julian days 52-122, with a mean duration of 70 days, the longest recorded for all the species during spring migration. Timing has a bimodal pattern, with a higher peak on Julian day 82 (SE=3.6 days) followed by a decrease that reaches a low in day 89 and a second peak on day 98. The annual variation in these patterns is substantial, and I found significant differences among years ($F_{2,36}=3.01$, $P<0.05$).

Fall migrations (mean $n=1,895,679$ individuals) are unimodal, with an approximately normal distribution and a well defined peak on day 291 (SE=2.8 days).

Ninety-five percent of the passage is recorded between days 270-323 and average duration is 53 days, significantly shorter than in spring ($t=2.79$, $df=9$, $P<0.01$). Survey dates truncate the late part of the season coverage for this species and extending field coverage to Julian day 334 (30 November) could cover the upper 95% quantile of the migration. Comparisons among fall seasons show this bird exhibits yearly differences ($F_{9,92}=1.01$, $P<0.05$), although most years, similar seasons are clustered in three groupings (t test for $LSD=1.92$, $df=9$, $P<0.05$).

Osprey (*Pandion haliaetus*). The early part of spring migration (mean $n=602$ individuals) is truncated by survey dates. The majority of the migrants (95%) are recorded between days 72-128 (mean duration 56 days) and their distribution has a unimodal pattern with a peak on day 99 ($SE=3.9$ days). Spring migration is significantly shorter in spring than fall migration ($t=4.29$ $df=9$ $P<0.001$), and I found differences in comparisons among years. ($F_{2,36}=3.01$, $P<0.05$)

Fall migration (mean $n=3,040$ individuals) has a unimodal pattern with a peak on day 274 ($SE=3.7$ days) and 95% of the individuals are recorded between days 238-312 (mean duration 74 days, the longest of all species in fall), although the end of the season distribution is truncated by survey dates. I found inter-annual differences in Osprey migration ($F_{9,92}=1.71$, $P<0.05$), and similarities among different field seasons are clustered in four groupings (t test for $LSD=1.58$, $df=9$, $P<0.05$).

Swallow-tailed Kite (*Elanoides forficatus*). The scarce and irregular spring migration records of this species (mean $n=8$ individuals) does not allow further discussion. Ninety-

five percent of the records are collected between days 86-130 (mean duration 44 days, with a peak on day 116 [SE=7.8 days]) and the distribution of these records is very different from year to year ($F_{2,36}=7.99$, $P<0.001$). Survey dates truncate the late part of the spring migration of this species and extending the migration season to Julian day 145 (25 May) covers most of the Swallow-tailed Kite migration season.

During the fall, the Swallow-tailed Kite (mean $n=162$ individuals) is the earliest of all fall migrants (95% of the migration recorded in a 42-day period between days 233-275). Current survey dates have a late start and do not allow complete coverage for this species, counts should be initiated in Julian day 213 (1 August) in order to include the majority of its migration. The peak number is recorded on day 235 (SE=1.6 days) shortly after the initiation of field seasons. This is one of the species with highest variation among years ($F_{9,92}=6.78$, $P<0.001$) and there are almost no similarities among years, clustered in eight groupings (t test for LSD=4.59, $df=9$, $P<0.001$).

Mississippi Kite (*Ictinia mississippiensis*). During spring migration (mean $n=21,062$ individuals), 95% of the Mississippi Kites are recorded between days 95-134 (39 days) with a peak on day 110 (SE=4.2 days). This is the last of the dominant species to pass through the region and the late part of its migration is not covered by current survey dates. As in the previous species, extending the count period to Julian day 145 (25 May) could cover most of the Mississippi Kite migration. I found significant differences among years in spring migration patterns ($F_{2,36}=5.99$ $P<0.01$).

Fall migration (mean $n=157,199$ individuals) is unimodal. Among dominant species, the Mississippi Kite is the earliest in the fall. Ninety-five percent of the migrants

are recorded over a 33-day period between days 237-270, with a peak on date 249 (SE=4.1 days), although the early part of the migration is truncated by survey dates (counts should start in Julian day 133 [10 August] to cover most of the fall migration). I found significant differences among years ($F_{9,92}=2.88$ $P<0.05$) and these differences are clustered in four groupings (t test for $LSD=2.01$, $df=9$, $P<0.01$).

Northern Harrier (*Circus cyaneus*). Its spring migrations (mean $n=69$ individuals) are scarce and irregular, with a platykurtic (flat-topped) distribution that obscures a seemingly bimodal distribution. Ninety-five percent of spring migrants are recorded over a 56-day period between days 60-116, significantly shorter than the fall period ($t=2.75$, $df=9$, $P<0.01$). The peak of this species' migration is on day 99 (SE=5.6 days) and I found significant differences among years ($F_{2,36}=4.89$, $P<0.05$).

During the fall (mean $n=447$ individuals), the migration period also shows a platykurtic, bimodal distribution and 95% of the migrations extend for a period of 70 days between days 252-322, with a low peak on day 291 (SE=4.9 days), and a slightly higher peak on day 309 (SE=3.1 days). The late part of the migration is truncated by survey dates and appropriate coverage for this species requires extending the counts to day 334 (30 November).

There are significant differences among field seasons ($F_{9,92}=2.49$ $P<0.01$) and similarities among them produce five groupings (t test for $LSD=3.78$, $df=9$, $P<0.001$).

Sharp-shinned Hawk (*Accipiter striatus*). Ninety-five percent of spring migration of this species (mean $n=598$ individuals) extends for a period of 56 days between days 75-131.

These flights are unimodal, with a peak on day 107 (SE=4.8 days). There are significant differences between years ($F_{2,36}=3.19$, $P<0.05$).

Fall migration (mean $n=4,280$ individuals) is unimodal, with a peak on day 285 (SE=4.1 days). The fall migration extends over a period of 52 days (95% of the total recorded) between days 267-319. I also found significant differences in inter-annual comparisons ($F_{9,92}=2.76$, $P<0.01$). Comparisons among groups cluster similar seasons in six groupings (t test for LSD=2.91, $df=9$, $P<0.01$).

Cooper's Hawk (*Accipiter cooperii*). During spring migration (mean $n=552$ individuals), this species exhibits a unimodal migration pattern with a leptokurtic (high-peaked) shape. The peak of migration for Cooper's Hawk is on day 96 (SE=3.8 days) and 95% of its migration is recorded between day 62-129, a period of 67 days (SE=3.9 days). I found statistically significant differences among spring seasons ($F_{2,36}=3.32$, $P<0.05$).

Fall migration (mean $n=2,433$ individuals) also has a unimodal distribution whose right tail is truncated by end of survey dates. Ninety-five percent of fall migrants are recorded between days 261-322, with a peak on day 287 (SE=3.1 days). The duration of the fall migration (61 days) is significantly shorter than the spring ($t=1.85$ $df=9$ $P<0.05$), but the late part of the migration is truncated by survey dates. Appropriate coverage for this species requires extending the counts to day 334 (30 November). I found statistically significant differences in inter-annual comparisons ($F_{9,92}=2.78$, $P<0.01$) and the similarities cluster seasons in six groupings (t test for LSD=2.84, $df=9$, $P<0.01$).

Broad-winged Hawk (*Buteo platypterus*). This is the most abundant migrant in spring and fall migration (spring mean n=319,094 individuals). Its spring migration pattern also shows an abrupt, leptokurtic pattern, with a peak on day 101 (SE=2.9 days). Ninety-five percent of the migration is recorded during a 43-day period between days 79-122, the shortest period of migration for all the species in spring. I found statistically significant differences in the spring seasonal timing ($F_{2,36}=3.33$, $P<0.05$).

Fall migration (mean n=1,931,255 individuals) also has the same unimodal, leptokurtic pattern with a peak on day 279 (SE=2.8 days). The majority of its migration (95%) can be recorded between days 257-291 (34 days) and fall migration is significantly shorter than spring ($t=1.99$ $df=9$ $P<0.01$). I found statistically significant differences among seasons ($F_{9,92}=1.56$, $P<0.05$) and these are clustered in three groups (t test for $LSD=1.55$, $df=9$, $P<0.05$).

Swainson's Hawk (*Buteo swainsoni*). Spring migration (mean n=105,403 individuals) is bimodal, with a first, slightly lower peak on day 88 (SE=2.1 days) and a second peak on day 111 (SE=2.8 days). The majority (95%) of the spring migration of this species can be recorded between days 72-116 and its duration is 44 days. I found significant differences between seasons ($F_{2,36}=3.21$, $P<0.05$).

Fall migration (mean n=812,419 individuals) is very different than spring. In fall, its migration pattern has a unimodal, leptokurtic pattern that peaks on day 290 (SE=2.6 days). The duration of fall migration is also significantly shorter, and 95% of the passage is recorded in only 20 days, the shortest of all species/seasons (days 279-299). I found statistically significant differences among seasons ($F_{9,92}=2.47$, $P<0.01$). Inter-annual

similarities in fall migration patterns are clustered in three groupings (t test for LSD=1.91, df=9, P<0.01). Among dominant species, the Swainson's Hawk is the last in the fall.

American Kestrel (*Falco sparverius*). Spring migration (mean n=1,004 individuals) is unimodal, with a peak on day 98 (SE=5.1 days). Ninety-five percent of the migration is recorded in a period of 43 days between days 73-119. Spring migration is significantly shorter than fall (t=0.99, df=9, P<0.05). I found statistically significant differences among seasons ($F_{2,36}=5.11$, P<0.01).

The fall migration (mean n=7,507 individuals), also has a unimodal pattern. Most of the individuals (95%) are recorded between days 261-317 (56 days), and fall peak is on day 281 (SE=5.1 days). I found significant differences among seasons ($F_{9,92}=0.59$, P<0.05) and seasons with similar patterns are clustered in six groupings (t test for LSD=1.88, df=9, P<0.01).

Merlin (*Falco columbarius*). The scarce and irregularly-spaced records of spring migration (mean n=27 individuals) do not show clear patterns to describe. Most of the migrants (95%) are reported between days 75-129, a 54-day period significantly shorter than fall migration with a peak on day 89 (SE=4.8 days) (t=4.11, df=9, P<0.001). As expected, I found significant inter-annual differences ($F_{2,36}=2.80$, P<0.01).

Fall migration (mean n=157 individuals) show an asymmetric, unimodal distribution, with a sharp increase to a peak on day 275 (SE=5.1 days). Ninety-five percent of the migrants are recorded in a 67-day period between days 255-322. I found

inter-annual differences ($F_{9,92}=2.41$, $P<0.01$). Similar seasons are clustered in six groupings (t test for $LSD=0.98$, $df=9$, $P<0.05$).

Peregrine Falcon (*Falco peregrinus*). Spring migration (mean $n=97$ individuals) has the same features of other falcons, with scarce and irregularly distributed records that extend for a 62-day period between days 70-132. This species has a slow increase, a sharp, abrupt first peak on day 86 ($SE=2.1$ days) and a second peak on day 118 ($SE=3.1$ days) followed by a sharp decline. The end of the spring migration is slightly truncated by survey dates and extending the field season to Julian day 145 (25 May) would cover most of their spring migration. I found significant differences among seasons ($F_{2,36}=2.10$, $P<0.05$).

During fall (mean $n=748$ individuals) 95% of the individuals are reported between days 257-318 (61 days), with a peak on day 278 ($SE=3.1$ days). The end of the fall migration is slightly truncated by survey dates. I found significant differences among fall seasons ($F_{9,92}=2.34$, $P<0.01$) and similar species are clustered in five groupings (t test for $LSD=4.44$, $df=9$, $P<0.001$).

Analysis of the species assemblage and species turnover.- The spring and fall patterns of the complete species assemblage are very different. During spring, migration is characterized by an early period of stasis between Julian days 50-72 with counts dominated by Turkey Vulture (DC 1 scores= 0.99-1.74). A period of stasis means one (or a few) species are dominant in the assemblage recorded at this time and the DC 1 scores are constant and graphically parallel to the X-axis (time) (Fig. 2).

During Julian days 76-121 there is a period of rapid species turnover that continues through the end of the survey dates. In this period, counts are dominated by Broad-winged Hawks (DC 1 scores=-0.03 - -0.17), Swainson's Hawk (DC 1 scores=1.1-2.15), and a late period dominated by Mississippi Kites (DC 1 scores= 1.37-2.25), but their numbers recorded in counts are not structured in a discernible pattern (ANCOVA $F_{2,36}=5.22$, $P<0.01$). Eigenvalue results of spring DCA are considerably different each year ($\lambda=0.236-0.491$) and far below a 'good fit' for the DCA model (Fig. 2).

The length of the axis during spring (amount of species turnover between the most dissimilar counts) ranged between 1.9 and 2.1 and is indicative of incomplete species turnover across the migration season. These values mean the species recorded in the early part of the spring are still found in the late part of the season, because an axis length of 4 indicates complete species turnover (Pielou 1984). These results also indicate that relationships between species in this assemblage are highly variable during spring migrations.

Low eigenvalues are attributable to the presence of more species with disparities in their seasonal timing and bimodal distributions that make the complete assemblage not fit the assumptions of the DCA statistical model. To test this statement, I ran additional DCA for the three years with spring data (1991, 1994, and 2004) using a simplified assemblage that contained only species with unimodal distributions (Fig. 1), and the eigenvalues found ranged from $\lambda=0.679-0.769$. This indicates assemblages that contain a high proportion of species with bimodal distributions are not a good fit for DCA.

The fall migration patterns of species turnover across the years have the clear stair-step pattern characteristic of an assemblage with clumped seasonal timing of

species. This means that in fall, migration comes in ‘waves’ of species/individuals that are followed by periods of uniform, lower species diversity dominated by a few (or a single) species. DCA axis 1 scores show alternating periods of stasis (horizontal, straight lines) and rapid species turnover (steep slopes of arriving waves of species). Three periods of stasis and two periods of rapid species turnover form a stair-step pattern. The first period of stasis is found early in the season between days 231-252 with counts dominated by early migrant Mississippi Kites (DC 1 scores=2.02-3.77) followed by one period of rapid turnover of species arriving between days 253-259, (e.g. Osprey [DC 1 scores=1.14-2.72], Merlin [DC 1 scores= 0.07-2.12] and Peregrine Falcon [DC 1 scores=0.32-2.19]).

Eigenvalues of fall DCA are similar for each year ($\lambda=0.859-0.974$) and the first DCA axis captures most of the variation (Figure 2). A second period of stasis has counts dominated by Broad-winged Hawk (DC 1 scores=0.12-2.32) and is followed by a second period of rapid species turnover between days 282-290 with arrival of species like Sharp-shinned Hawk (DC 1 scores 0.02-1.68), Cooper’s Hawk (DC 1 scores= 0.00-1.57) and American Kestrel (DC 1 scores= 0.05-2.04). The final period of stasis is dominated by counts of Turkey Vulture (DC 1 scores=0.00-0.28 and Swainson’s Hawk (DC 1 scores=-0.01-0.00) until the end of the counts on Julian day 324. Box-Cox transformed values of DC 1 axis scores yield no significant differences among years (ANCOVA $F_{9,92}=2.99$, $P=n.s.$).

The length of the axis during spring ranged between 2.1 and 3.8 and these higher scores are indicative of more species turnover across the migration season (species composition of early season counts is almost completely different than late season

counts). In both spring and fall migration periods, the seasonal timing of individual species is highly variable among years (Table 1). The relative position of species in this assemblage remains fairly constant, which means the sequence of arrival and departure has few changes across years (Fig. 3).

DISCUSSION

The timing of species' migration varies annually. Significant variation in the seasonal timing occurs both within and among years (Fig. 1). Species arrive, peak, and depart within a time period that is predictable within certain limits, although some major differences across the years can be noticed. Although the analysis of spring data using DCA shows no discernible pattern, the analysis for the fall season has a clear stair-step shape of assemblages with clumped temporal distributions. Fall assemblage patterns are not significantly different among years.

Identifying the processes behind differences in intra- and inter-annual vulture and raptor migration patterns has been a challenging task (Richardson 1978, Titus and Mosher 1982, Smith 1985, Woodrey and Chandler 1997). Many studies have documented the influence of proximate factors (fide Gauthreaux 1996:446) on migration patterns. These include (1) Weather effects (favorable conditions are positively correlated with larger amounts of migrants e.g. Mueller and Berger 1961, Kerlinger and Moore 1989, Hall et al. 1992); (2) Differences in migration ecology of sex and age classes (juveniles migrating at different dates/locations than adults result in species with bimodal or unclear migration patterns, e.g. Mueller and Berger 1967, Bildstein et al. 1984, Woodrey and Chandler 1997, DeLong and Hoffman 1999, Thorup et al. 2003); (3)

Diet (species feeding on resources that become scarce earlier in the year, such as insects, fruit, and cold-blooded prey, tend to depart breeding areas earlier, Newton 1979, Leshem and Yom-Tov 1996); (4) Size and location of breeding and wintering areas (species with longer distances between breeding and wintering areas migrate earlier in the south-bound migration and return later in the north-bound flights, e.g. Hagan et al. 1991, Newton and Dale 1997); and perhaps (5) Interspecific competition (species with similar ecological requirements segregate both spatial and temporally, Francis and Cooke 1986, Moore and Yong 1991), among others. Most of these reports recognize problems of colinearity among the variables listed above (e.g. Hall et al. 1992, Hoffman and Smith 2003, Berthold 2001).

I will not attempt to establish direct correspondence between different variables and the migration patterns observed and quantified. Instead, I will focus on making a distinction between variables that have effects at different scales, in the patterns observed among species and the complete assemblage.

Proximate factors can explain the variation observed within species among years (e.g. species are expected to have different patterns every year because of different inter-annual weather patterns, Allen et al. [1996]), and these associations have been elucidated in some recent studies (Elkins 1983, Gauthreaux 1996, Niles et al. 1996).

Variables such as large-scale weather patterns with effects of larger magnitude, operate at the other extreme of the scale gradient and are more likely to influence the patterns of migration of all species and affect the structure of the data for the assemblage (Hüppop and Hüppop 2003). The effect of these variables is more likely to be observed in the relative distance among species during the season and the phenological sequence of

species in the assemblage. Assemblage-wide patterns may exhibit a higher degree of conservatism over time and would therefore have little or no difference in a period of a few years (Ketterson and Nolan 1985, Berthold 2001, Visser and Both 2005).

This statement is supported by the lack of differences among assemblage turnover patterns in DC 1 axis scores across ten years of fall data. Among species, however, I found different degrees of similarity in fall migration patterns. I can not explain why in some species the number of groupings in orthogonal comparisons yielded more clusters than in others (ranging from three in Turkey Vulture to eight in Swallow-tailed Kites), but authors like Berthold (2001:77), and Shamoun-Baranes et al. (2003) suggest that species with shorter migration distances would have more seasonal variation than long-distance migrants. I do not have specific information on the distance these migrants are covering between breeding and wintering areas to test this hypothesis even roughly, but it seems reasonable to think that long-distance migrants would have more consistent patterns among years.

Quantifying species-assemblage patterns is important for understanding larger scale factors affecting bird migration. This fact has been recognized in recent papers documenting shifts in the phenology of many ecological processes, including bird migration (Pulido et al. 2001, Noordwijk 2003), and Visser and Both (2005) reiterate the importance of quantitative baseline data across multiple taxa for long-term monitoring of large-scale processes such as global warming.

My results also suggest there is a need to adjust the range of dates used in analyses of populations trends, to accommodate for this variation, and to not 'fix' the period of a field season to be used in calculating population indices (Chapter 4).

In summary, my research shows that the seasonal timing of species in spring and fall is variable both within and between years, with dates of seasonal timing varying within certain limits. The dispersed structure of the spring data sets does not allow making further inferences on the possible role of local versus range-wide effects in migration, but fall data suggests that the structural patterns observed by the complete assemblage of species are modeled by the effect of large-scale (range-wide) variables that shape its annual patterns.

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Table 1. Average temporal distribution properties of spring and fall migration of 12 species of migrant vultures and raptors in Veracruz, Mexico (\bar{x} Julian day [Roman date], spring n=3 field seasons, fall n=10 field seasons).

Species [Alpha code] <i>Scientific name</i>	Spring		
	Lower 95% quantile ¹	Peak	Upper 95% quantile ²
Turkey Vulture [TUVU] <i>Cathartes aura</i>	52 (21 Feb) ¹	82 (23 Mar)	122 (2 May)
Osprey [OSPR] <i>Pandion haliaetus</i>	72 (13 Mar)	99 (9 Apr)	128 (8 May)
Swallow-tailed Kite [STKI] <i>Elanoides forficatus</i>	86 (27 Mar)	116 (26 Apr)	130 (10 May) ²
Mississippi Kite [MIKI] <i>Ictinia mississippiensis</i>	95 (5 Apr)	110 (20 Apr)	134 (14 May) ²
Northern Harrier [NOHA] <i>Circus cyaneus</i>	60 (1 Mar)	99 (9 Apr)	116 (26 Apr)
Sharp-shinned Hawk [SSHA] <i>Accipiter striatus</i>	75 (16 Mar)	107 (17 Apr)	131 (11 May)
Cooper's Hawk [COHA] <i>Accipiter cooperii</i>	62 (3 Mar)	96 (6 Apr)	129 (9 May)
Broad-winged Hawk [BWHA] <i>Buteo platypterus</i>	79 (20 Mar)	101 (11 Apr)	122 (2 May)
Swainson's Hawk [SWHA] <i>Buteo swainsoni</i>	72 (13 Mar)	111 (21 Apr)	116 (26 Apr)
American Kestrel [AMKE] <i>Falco sparverius</i>	73 (14 Mar)	98 (8 Apr)	119 (29 Apr)
Merlin [MERL] <i>Falco columbarius</i>	75 (16 Mar)	89 (30 Mar)	129 (9 May)
Peregrine Falcon [PEFA] <i>Falco peregrinus</i>	70 (11 Mar)	118 (28 Apr)	132 (12 May) ²

Species	Fall		
	Lower 95% quantile ¹	Peak	Upper 95% quantile ²
Turkey Vulture	270 (27 Sep)	291 (18 Oct)	323 (19 Nov) ²
Osprey	238 (26 Aug)	274 (1 Oct)	312 (8 Nov)
Swallow-tailed Kite	233 (21 Aug) ¹	235 (23 Aug)	275 (2 Oct)
Mississippi Kite	237 (25 Aug) ¹	249 (6 Sep)	270 (27 Sep)
Northern Harrier	252 (9 Sep)	309 (5 Nov)	322 (18 Nov) ²
Sharp-shinned Hawk	267 (24 Sep)	285 (12 Oct)	319 (15 Nov)
Cooper's Hawk	261 (18 Sep)	287 (14 Oct)	322 (18 Nov) ²
Broad-winged Hawk	257 (14 Sep)	279 (6 Oct)	291 (18 Oct)
Swainson's Hawk	279 (6 Oct)	290 (17 Oct)	299 (26 Oct)
American Kestrel	261 (18 Sep)	281 (8 Oct)	317 (13 Nov)
Merlin	255 (12 Sep)	275 (2 Oct)	322 (18 Nov)
Peregrine Falcon	257 (14 Sep)	278 (5 Oct)	318 (14 Nov)

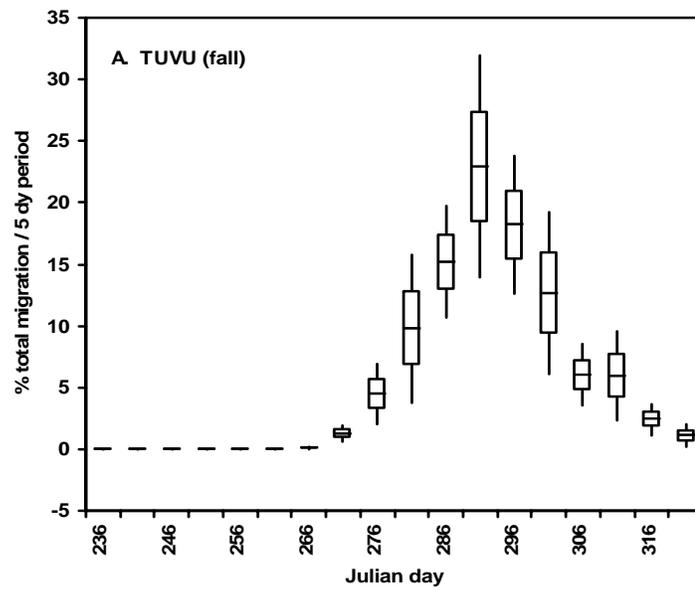
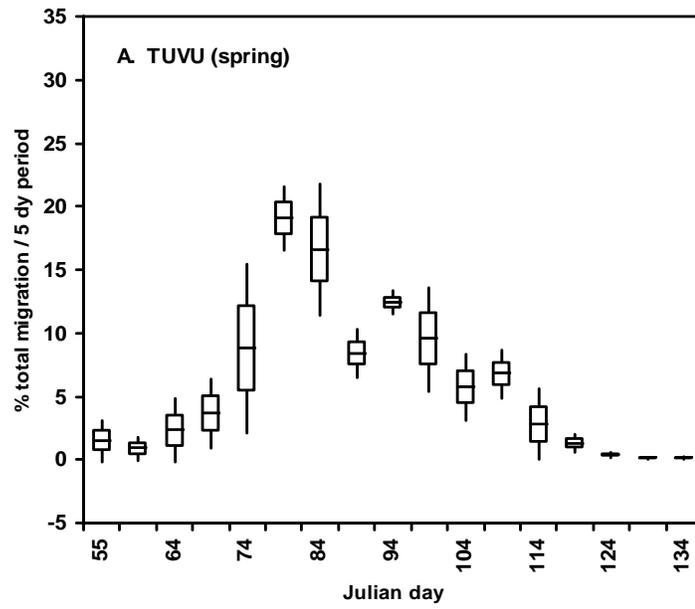
¹ Early part of migration truncated by count dates; ² Late part of migration truncated by count dates. In order to improve the spring coverage of the seasonal timing of migration for these species, spring counts should start on Julian day 41 (10 February) to include the complete migration of Turkey Vultures, and to finish those counts until at least Julian day 145 (25 May) to cover Peregrine Falcon, Swallow-tailed and Mississippi Kite migration. Coverage in the fall should be initiated in Julian day 213 (1 August) in order to include the majority of Swallow-tailed Kite migration and Julian day 133 (10 August) to cover Mississippi Kite migration. The fall season should also be extended until Julian day 334 (30 November) to cover the end of the migration season for Turkey Vulture, Northern Harrier, and Cooper's Hawk.

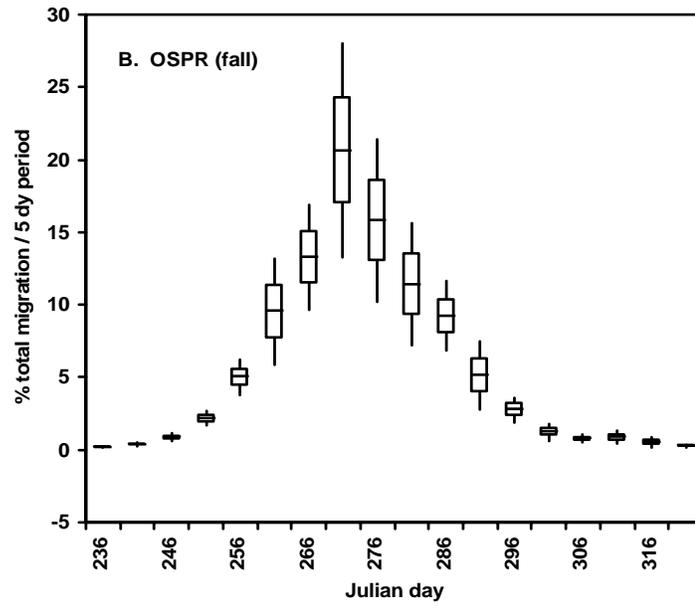
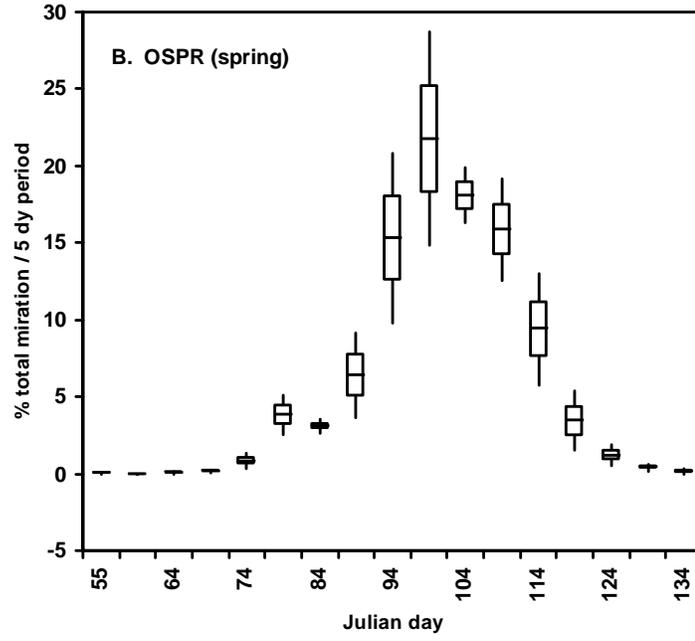
FIGURE LEGENDS

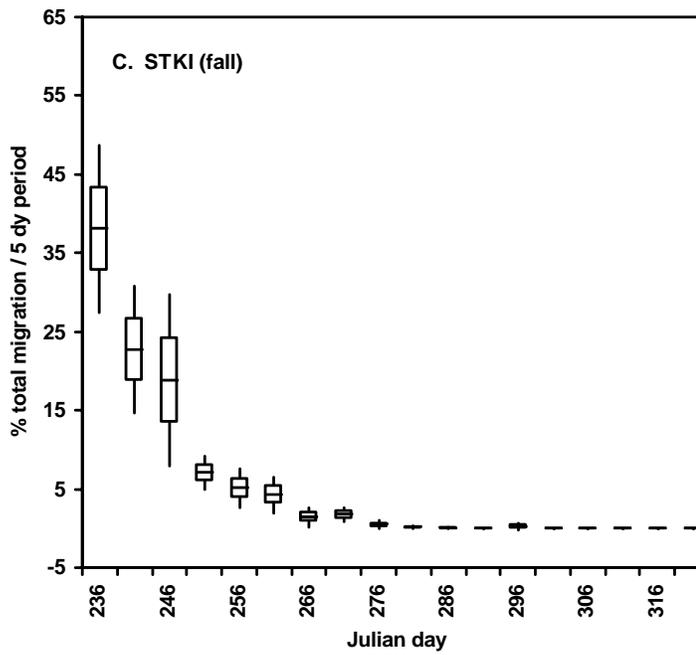
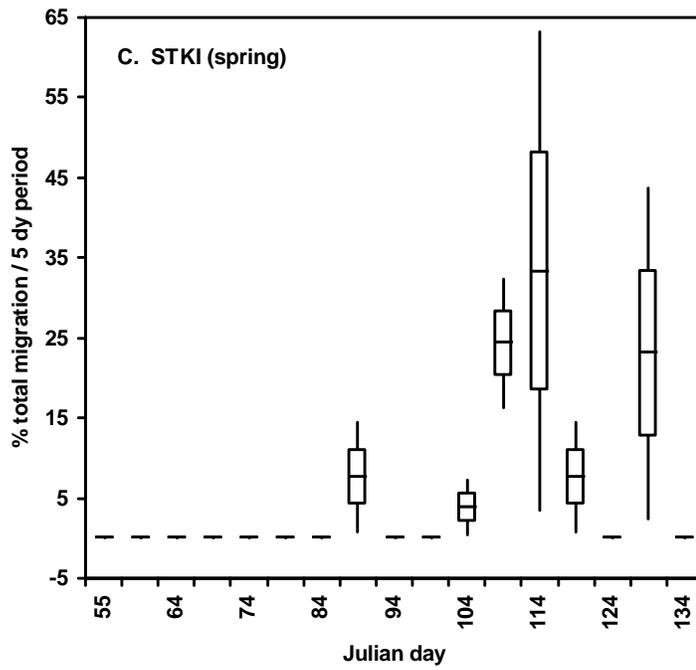
Figure 1. Seasonal timing of 12 vulture and raptor species in Veracruz, Mexico (\bar{x} , standard error, and 95% confidence intervals). Spring migration data (left column, n=3 field seasons, 1991, 1994, 2004) was collected between 20 February – 15 May (Julian days 51-135); and fall migration data (right column, n=11 field seasons 1992, 1993, 1995, 1996, 1998-2004) was collected between 20 August – 20 November (Julian days 232-324). Species included (with alpha code) are: (a) Turkey Vulture (TUVU); (b) Osprey (OSPR); (c) Swallow-tailed Kite (STKI); (d) Mississippi Kite (MIKI); (e) Northern Harrier (NOHA); (f) Sharp-shinned Hawk (SSHA); (g) Cooper's Hawk (COHA); (h) Broad-winged Hawk (BWAH); (i) Swainson's Hawk (SWHA); (j) American Kestrel (AMKE); (k) Merlin (MERL), and (l) Peregrine Falcon (PEFA).

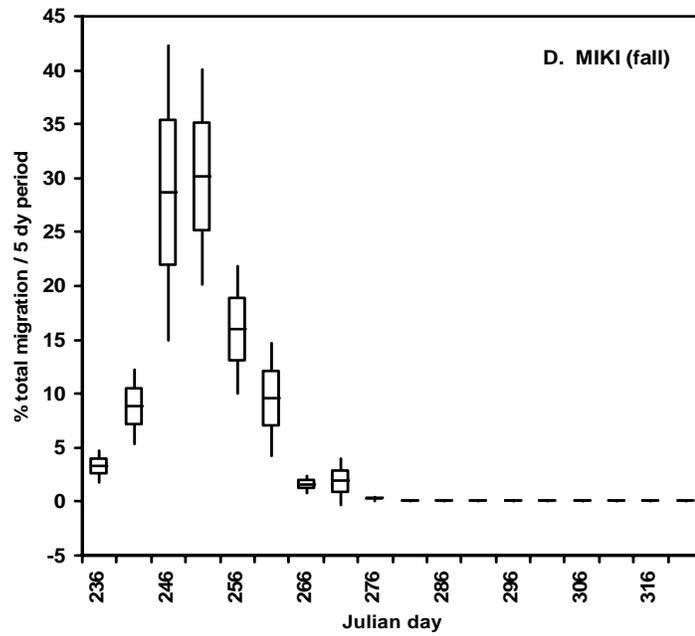
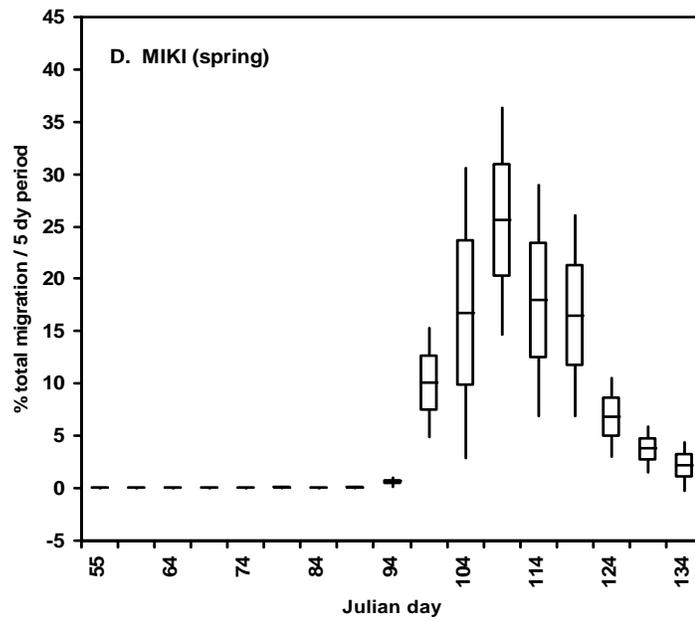
Figure 2. Patterns of migration in an assemblage of one species of New World vulture and 11 species of raptors through central Veracruz, Mexico illustrated by Detrended Correspondence Analysis axis 1 scores plotted against Julian day for spring and fall migration. Spring patterns ($\lambda=0.236-0.491$, length=1.9-2.1, $r=0.000$ n.s.) are for the period between Julian days 51 (20 Feb)-135 (15 May). Fall patterns ($\lambda=0.859-0.974$, length=2.1-3.8, $r=0.000$ $P<0.001$) correspond to the period between Julian days 232 (20 August)-324 (20 November).

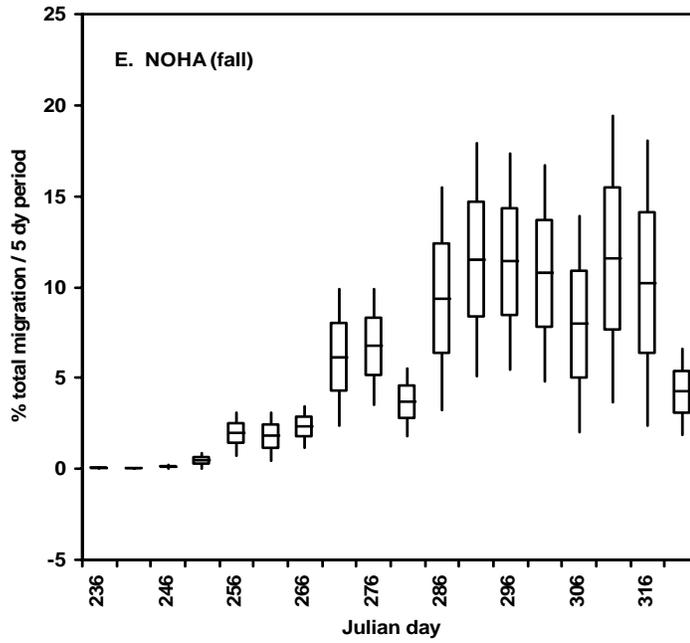
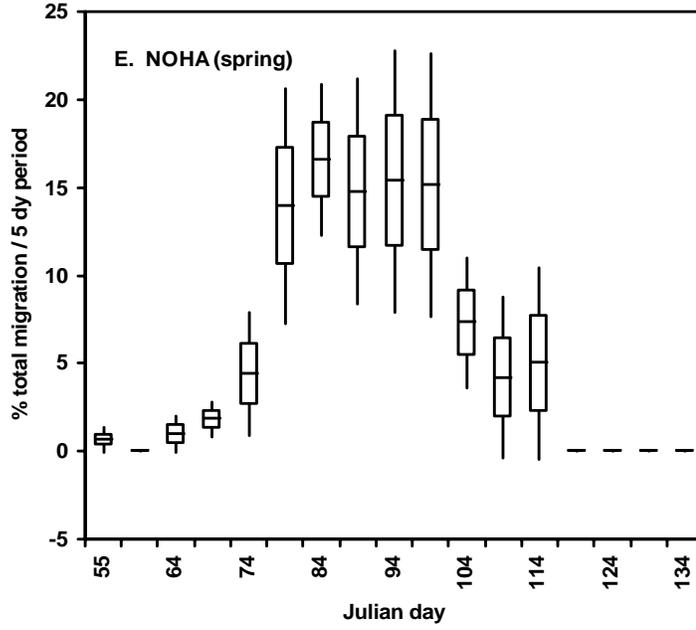
Figure 3. Sequence of migration of an assemblage of vulture and raptor species in Veracruz, Mexico, as determined by species scores in Detrended Correspondence Analysis Axis 1 (DCA axis 1). DCA axis 1 values determine the position and relative distance in the phenology of migration (species alpha codes in Fig.1).

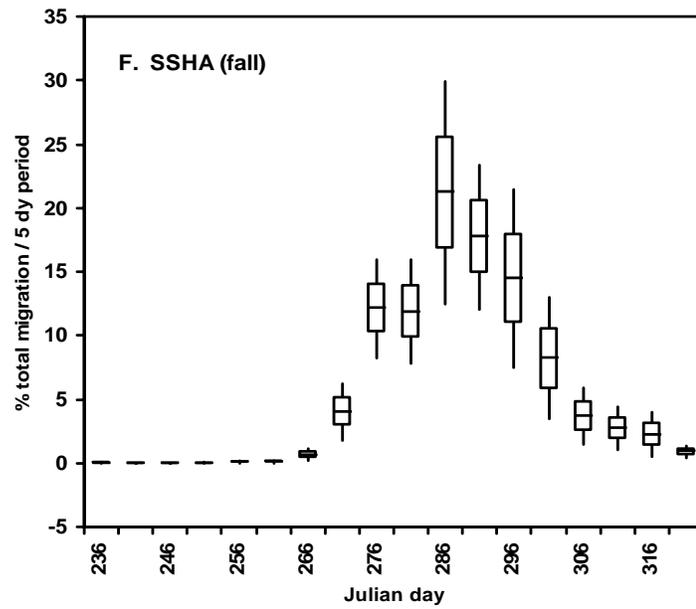
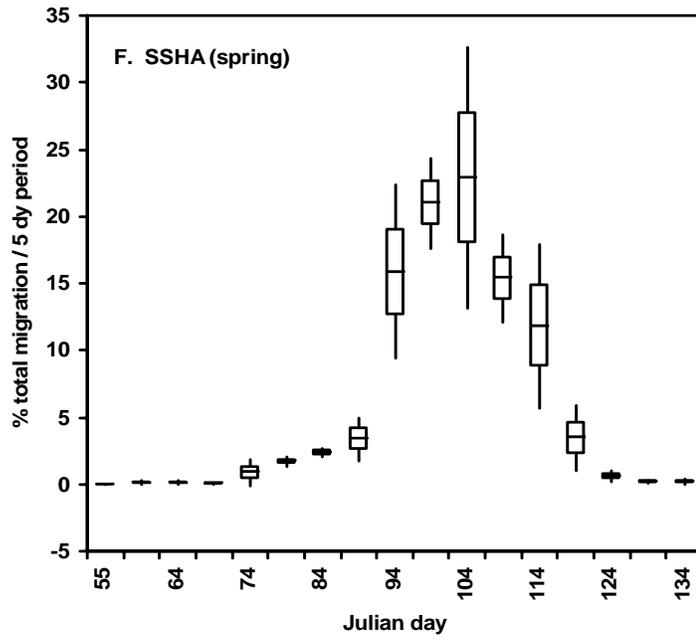


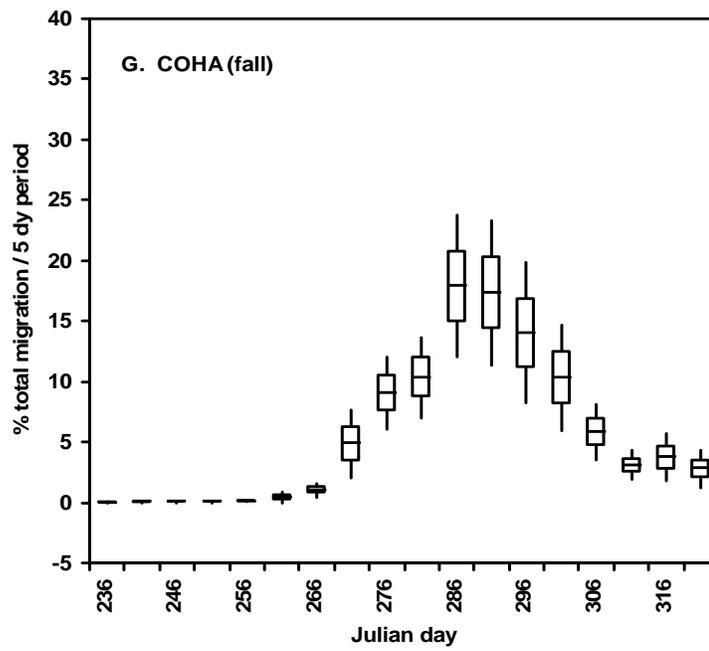
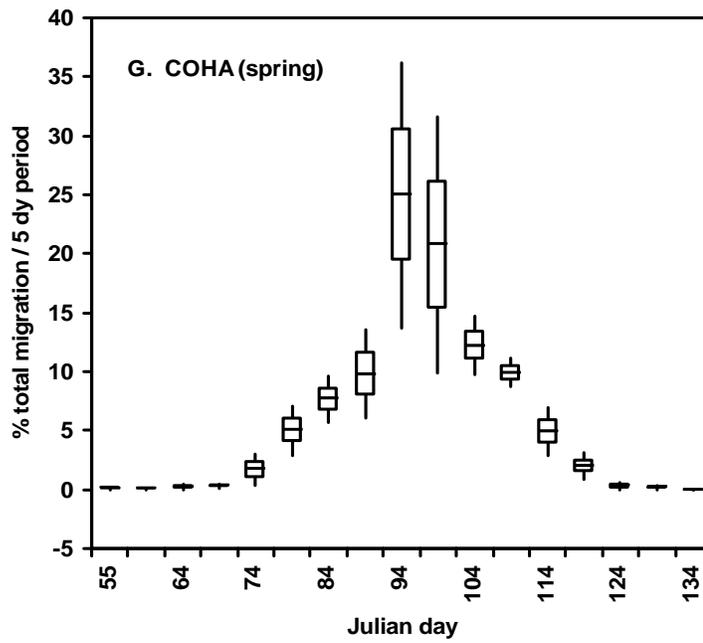


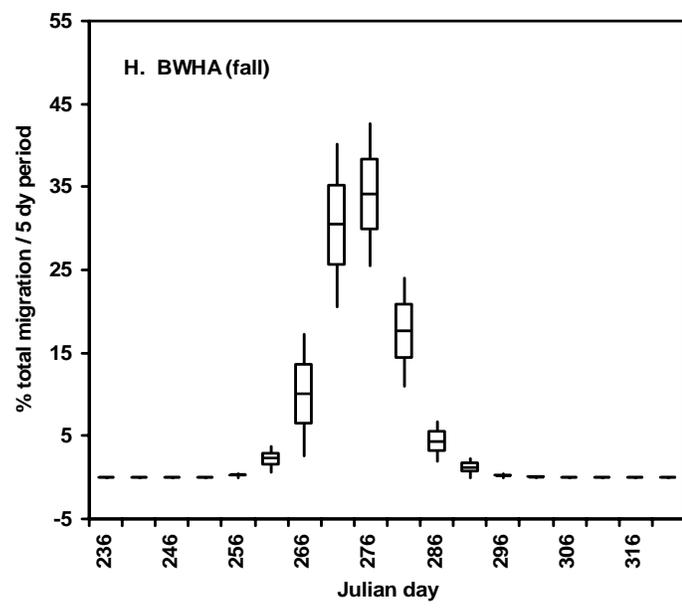
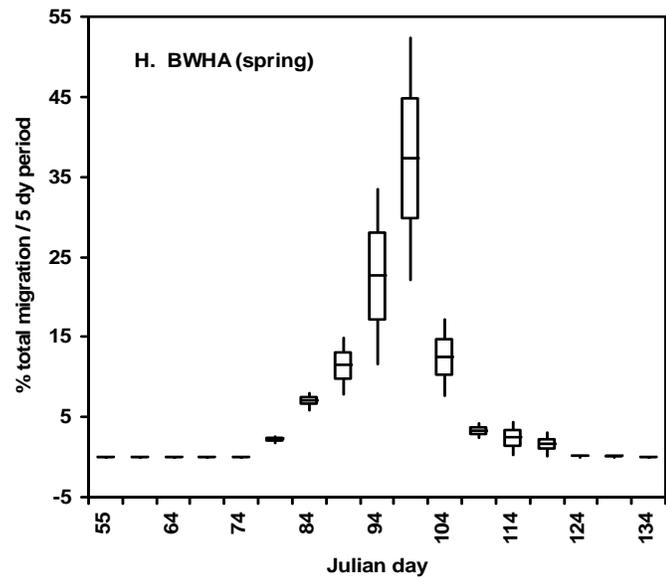


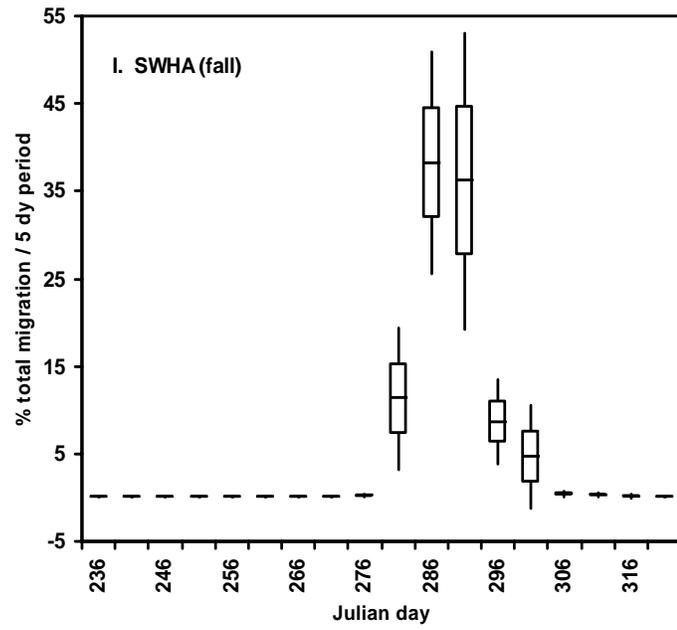
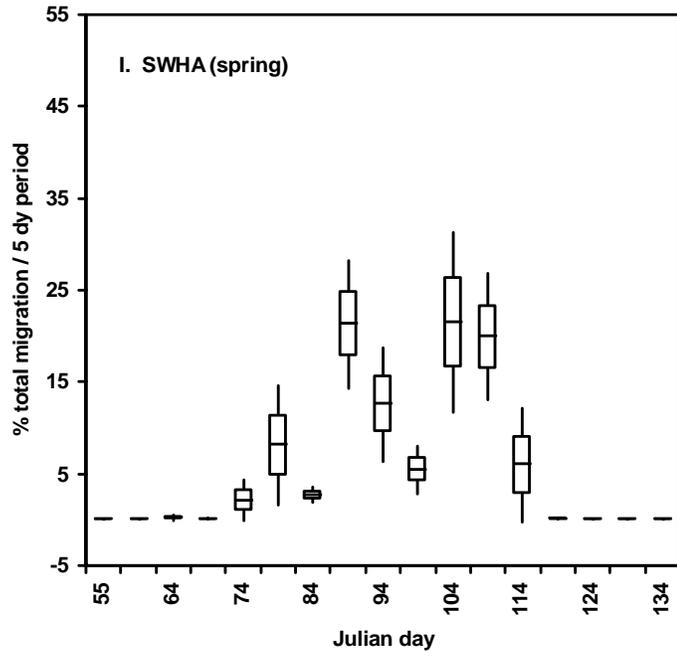


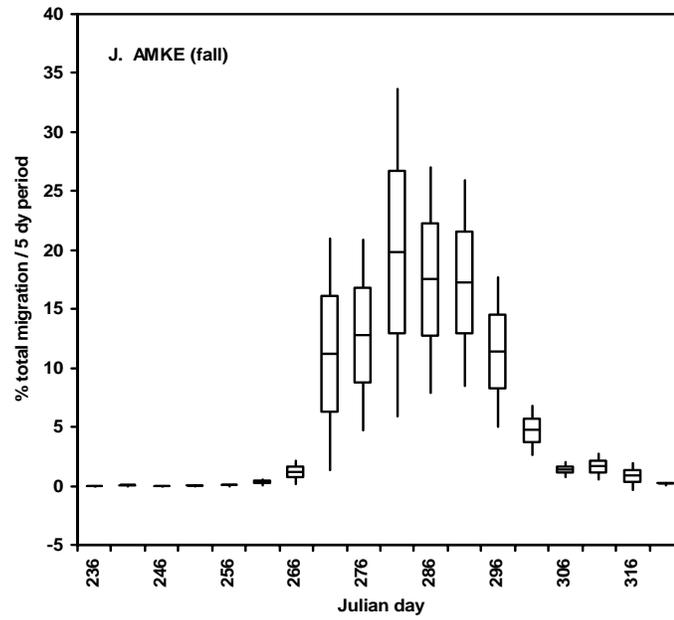
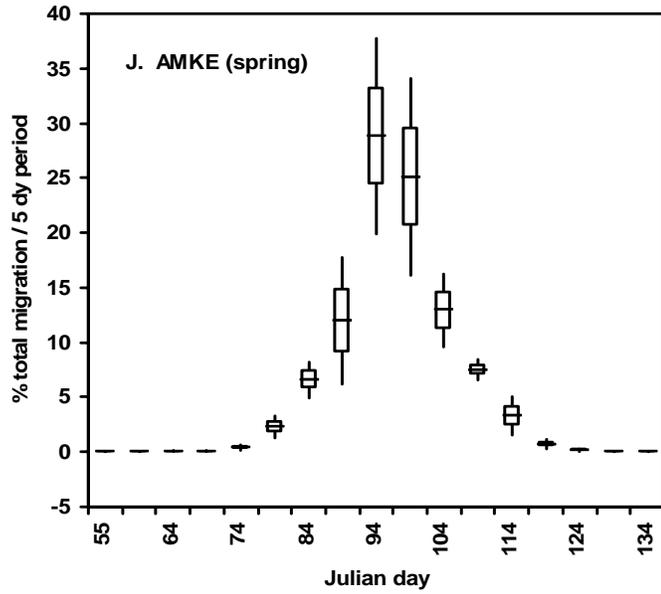


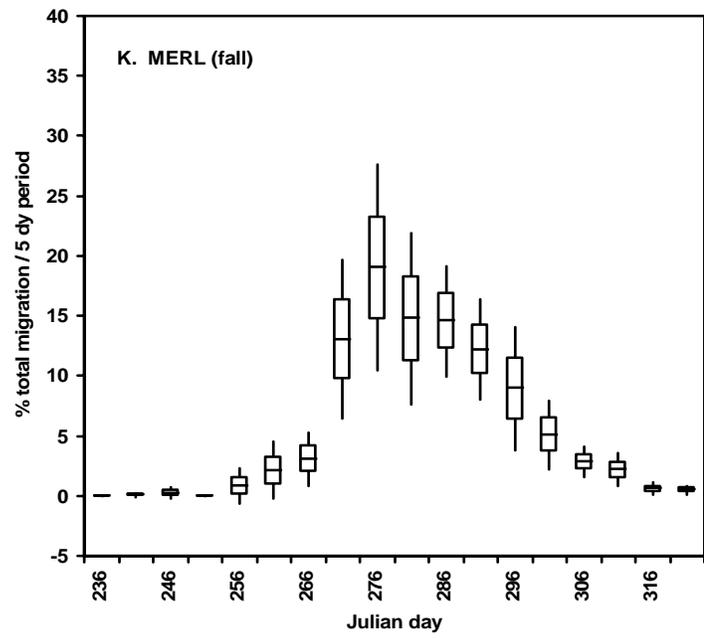
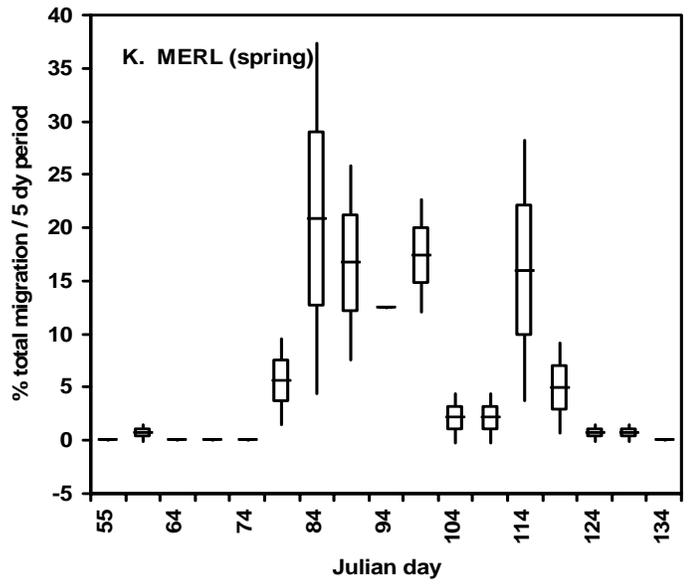


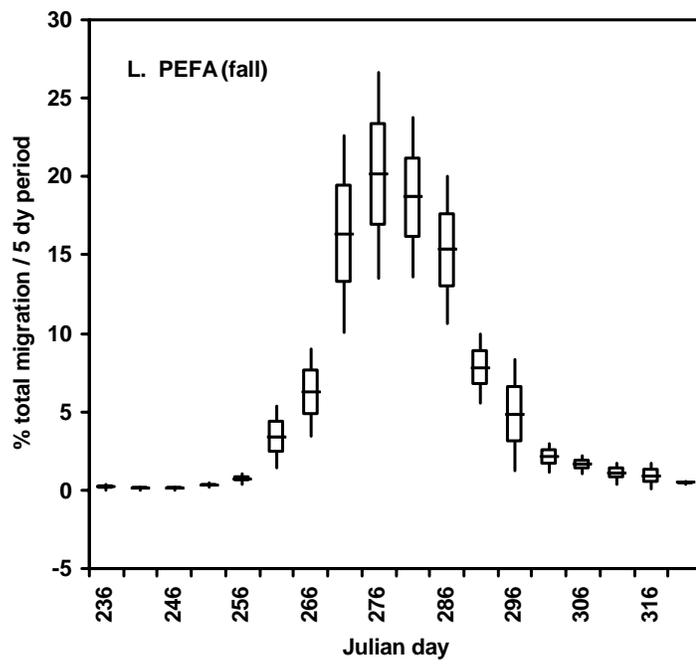
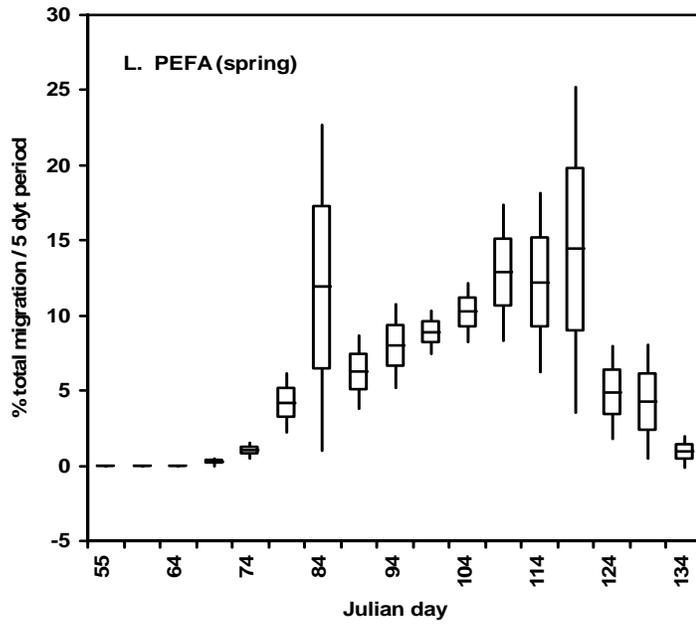




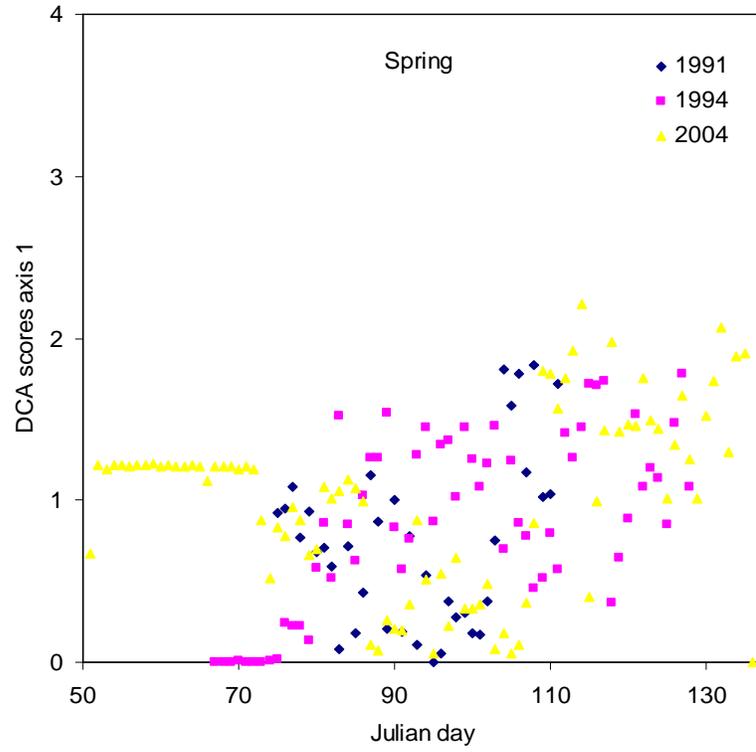




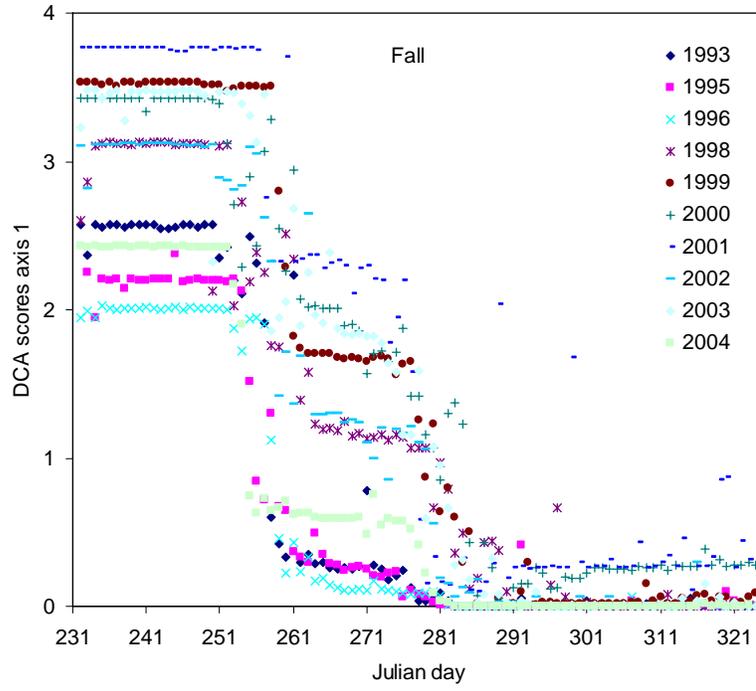




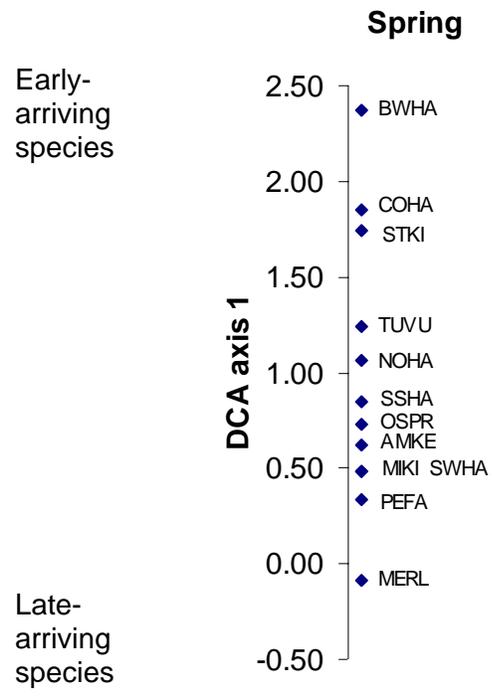
(Fig.2)



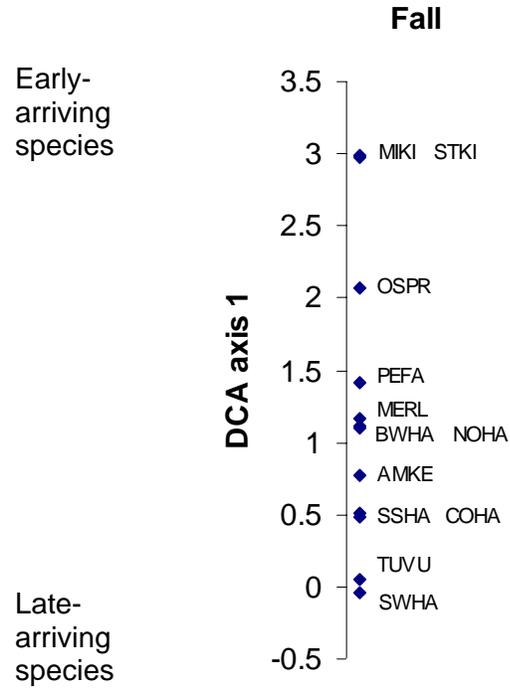
(Fig. 2, cont.)



(Fig. 3)



(Fig. 3, cont.)



CHAPTER 3

BEHAVIOR AND FLIGHT PERFORMANCE OF THERMAL-SOARING MIGRANTS

Abstract.- Many diurnal migrants use thermal-soaring flight during cross-country movements. To quantify the differences in flight performance among species and migration seasons, I studied the behavior of nine species of large soaring birds at a geographic bottleneck for migrants and quantified their wing beat frequency, a commonly used measure of flight performance. There are significant differences among species' wing beat frequency, and larger birds tend to require less energetic expenditure in their flights. I also found seasonal differences in wing beat frequency in seven species, and, contrary to my predictions, spring is a season that demands higher energetic expenditure (higher wing beat frequency) for more species than fall. Because of lack of other information such as wing load data and flight speed, I was unable to compare results of this empirical research with existing theoretical models to calculate wing beat frequency.

Key words: Behavior, flight performance, wing beat frequency, thermal-soaring migrants.

INTRODUCTION

Thermal-soaring is a mode of assisted locomotion for cross-country flights favored by many large, diurnal, migrating birds (Chapter 1). The mechanics of this process were described over 35 years ago along with supporting theoretical models (Pennycuick 1969, 1975, 1998). Birds locate unevenly distributed atmospheric convection and turn tight circles around uprising thermals. After climbing the maximum height possible, migrants exit the thermal and glide in their desired flight direction in a gradual sink. When migrants have lost height, they locate a new thermal and start the process again (Pennycuick 1969, 1998).

The flight behavior of thermal-soaring birds is a highly plastic feature that is constantly adjusted to maximize distance traveled and minimize energetic expenditure (Kerlinger 1989, Spaar 1997, Spaar and Bruderer 1996, 1997, Bruderer et al. 2001). Two important changes occur in migrants' flight behavior in response to patchy spatial and temporal distribution of atmospheric uplift: (1) Birds form flocks to facilitate the location of thermals (Kerlinger 1985), and (2) Migrants change the rate of wing beat frequency to adjust for body drag in relation to thermal lift (Kerlinger and Moore 1989, Leshem and Yom-Tov 1996).

Here I examine changes in wing beat frequency (f) in thermal-soaring, diurnal migrants. Wing beat frequency is a measure of flight performance in studies of birds in cross-country flights (Pennycuick 1978, 1989, 2001). Flight performance is improved when migrants require a low energetic expenditure (low f) to make use of thermal lift in cross-country flights (Pennycuick 1972, 1975, Hedenström 1993). If this assumption is correct, and considering thermal convection in Veracruz is higher in spring than in fall

(Chapter 1), my prediction is that migrants will have a higher flight performance during spring, and will exhibit a comparatively lower wing beat frequency.

Here I measure wing beat frequency in nine species of thermal-soaring migrants. I compare the relative effort among species and among migration seasons and relate my results to my prediction and to other theoretical and empirical measures of flight performance that may explain differences found.

METHODS

I made observations of flight behavior during spring and fall migration seasons, at a field site located along a major migration route (Ruelas et al. 2000). Central Veracruz, Mexico, is located at the intersection of two major mountainous systems, the Sierra Madre Oriental and the central volcanic belt. These two mountain ranges constrain the width of the Gulf coastal plain to a narrow geographic bottleneck used by many species of thermal-soaring migrants (Chapter 1).

During spring migration, I collected data from two localities, Rinconada ($19^{\circ}21'N$ - $96^{\circ}34'W$, elevation 313 meters above the sea level [hereon mASL]) and Cerro Gordo ($19^{\circ}26'N$ - $96^{\circ}42'W$, elevation 660 mASL) from 20 February – 15 May 2004. During fall migration, I collected observations from Chichicaxtle ($19^{\circ}21'N$ - $96^{\circ}28'W$, elevation 120 mASL) and Cardel ($19^{\circ}22'N$ - $96^{\circ}22'W$, elevation 29 mASL) from 20 August – 20 November 2004 (more information on localities, a description of the study area, and data collection protocols during migration counts is available in Chapter 1 and in Ruelas et al. 2005).

My field assistants and I selected one transient migrant at a time, either during the thermal-climbing or the inter-thermal gliding period of flight, and tallied its wing beat frequency (f) during 30-second focal observations using a hand chronometer. We collected as many focal observations as possible during the daily observation period of migration counts, 0800-1800 hrs. CST. In order to determine differences in flight performance among seasons and species, I selected those for which I had more than 30 observations per site per season, and calculated the season mean, 95% confidence intervals, and made statistical test comparisons to determine differences in seasonal observations.

RESULTS

My assistants and I collected over 18,000 focal observations of nine species of soaring migrants during the spring ($n=7,652$) and fall ($n=10,712$) of 2004. Here, I report the observed mean wing beat frequency values and compare the flight performance of each species in spring and fall. Species marked with an asterisk have statistically significant differences among seasons (Fig. 1).

Anhinga (*Anhinga anhinga*).* During spring migration, the Anhinga's mean wing beat frequency is 9.6 min^{-1} ($SD=9.8$, $n=33$ observations). This contrasts with a higher flight performance in the fall when a lower wing beat frequency is observed (mean= 2.7 min^{-1} , $SD=6.2$, $n=83$ observations) ($t=4.49$, $df=114$, $P<0.0001$).

Turkey Vulture (*Cathartes aura*).* This species has the highest flight performance for thermal-soaring among all species in both seasons. In spring, the mean wing beat frequency is 0.7 min^{-1} (SD=3.0, n=2,977 observations). Turkey Vulture's flight performance is significantly higher in the fall, when the mean wing beat frequency is lower (mean= 0.4 min^{-1} , SD=5.2, n=3,701 observations) ($t=7.98$, $P<0.0001$).

Osprey (*Pandion haliaetus*).* The mean spring wing beat frequency of the Osprey is 3.2 min^{-1} (SD=7.5, n=243 observations), lower than the frequency observed in the fall (mean= 5.7 min^{-1} , SD=10.5, n=181 observations) ($t=-2.75$, $df=422$, $P=0.0063$).

Mississippi Kite (*Ictinia mississippiensis*).* The flight performance of this kite is significantly higher in spring (mean wing beat frequency= 2.2 min^{-1} , SD=5.0, n=880 observations). During fall migration, the mean wing beat frequency observed is 1.6 min^{-1} (SD=3.8, n=3,674 observations) ($t=3.92$, $P<0.0001$).

Sharp-shinned Hawk (*Accipiter striatus*).* In spring, the flight performance is higher, with a mean wing beat frequency of 8.8 min^{-1} (SD=6.0, n=88 observations). In the fall, mean wing beat frequency is 13.3 min^{-1} (SD=10.5, n=37 observations) ($t=-2.78$, $df=112$, $P=0.0064$).

Cooper's Hawk (*A. cooperii*). The flight performance of the Cooper's Hawk is very similar in spring and fall. Spring wing beat frequency is 7.4 min^{-1} (SD=7.3, n=86 observations), while in the fall, mean wing beat frequency is 7.5 min^{-1} (SD=7.7, n=44 observations) ($t=0.0088$, $df=128$, $P=0.99$, n.s.).

Broad-winged Hawk (*Buteo platypterus*). This species also has very similar flight performance in both seasons. In spring, the mean wing beat frequency is 1.3 min^{-1} (SD=2.7, n=2,363 observations). During the fall, mean wing beat frequency is also 1.3 min^{-1} (SD=2.7, n=2,282 observations) ($t=0.0029$, $P=0.32$, n.s.).

Swainson's Hawk (*B. swainsoni*).* The spring flight performance of the Swainson's Hawk is lower than its flight performance in the fall. In spring, mean wing beat frequency is 1.2 min^{-1} (SD=2.5, n=824 observations). In the fall, mean wing beat frequency is reduced to 0.7 min^{-1} (SD=2.7, n=670 observations) ($t=-3.67$, $P=0.0003$)

American Kestrel (*Falco sparverius*).* This species has the lowest flight performance for thermal-soaring flight among all the species in both seasons. In spring, performance is lower than in fall, with a mean wing beat frequency of 19.7 min^{-1} (SD=13.3, n=158 observations). During fall, the mean wing beat frequency is lower (17.5 min^{-1} , SD=13.4, n=40 observations) ($t=-0.394$, $df=110$, $P=0.69$).

DISCUSSION

During cross-country flights, migratory birds exhibit different flight performance among species and migration seasons. Pennycuick (1996) has created three arbitrary categories to classify species along different positions in a continuum. The extremes of this gradient are: (1) Gliding, (2) Powered flight, and the intermediate strategy is termed (3) Powered glide.

Among species, I found a >35-fold difference in the wing beat frequency recorded. Why do some species have higher flight performance than others? Pennycuick (1972, 1978, 1990, 1996), Pennycuick et al. (1996), and Hedenström (2003), have studied this issue in great detail, using large and small birds both in theory and in field and controlled experiments using wind tunnels. These authors found that species with lower wing loads (the ratio between wing area and body mass) require less energetic expenditure in cross-country flights. This low energetic expenditure may be so significant to may enable some large species of birds to fly significant portions of their migration without feeding (Smith et al. 1986).

I attempted to test this with my field data, but lack of information on wing loads on many species, and the difficulty to use data collected by other authors under different criteria, prevented me from exploring this issue any further (Poole et al. 1938, Clark 1971, Evered 1990, Winker 1998, Stiles and Altshuler 2004). Instead, I found that with the exception of Anhinga, birds with lower body mass had a tendency to have lower flight performance.

The differences in the spring and fall flight performance found on seven species are contrary to my expectations. In five of these species (Anhinga, Turkey Vulture, Mississippi Kite, Swainson's Hawk, and American Kestrel) spring migration wing beat frequency was higher (lower flight performance) than in fall, and only two species, Osprey and Sharp-shinned Hawk had higher flight performance in spring. Two species (Broad-winged Hawk and Cooper's Hawk) had similar wing beat frequencies among seasons.

These results indicate that although higher thermal convection may facilitate cross-country flights during a migration season, this fact does not necessarily mean birds will have a lower energetic expenditure.

Why do species have more thermal uplift available in spring and still have flights of a higher energetic cost? I do not have a definite answer on this question. Researchers have documented differences in duration of migration seasons and have interpreted these as a response to the need to arrive earlier to breeding territories (Berthold 2001). This could create the need for faster spring migrations at higher energetic cost, but without information on the origin and destination of migrants and its rate of travel this hypothesis can not be tested. Other information is required to contrast these empirical observations of wing beat frequency with theoretical estimations developed by Pennycuik (1990, 1996) and the most recent done by Nudds et al. (2004).

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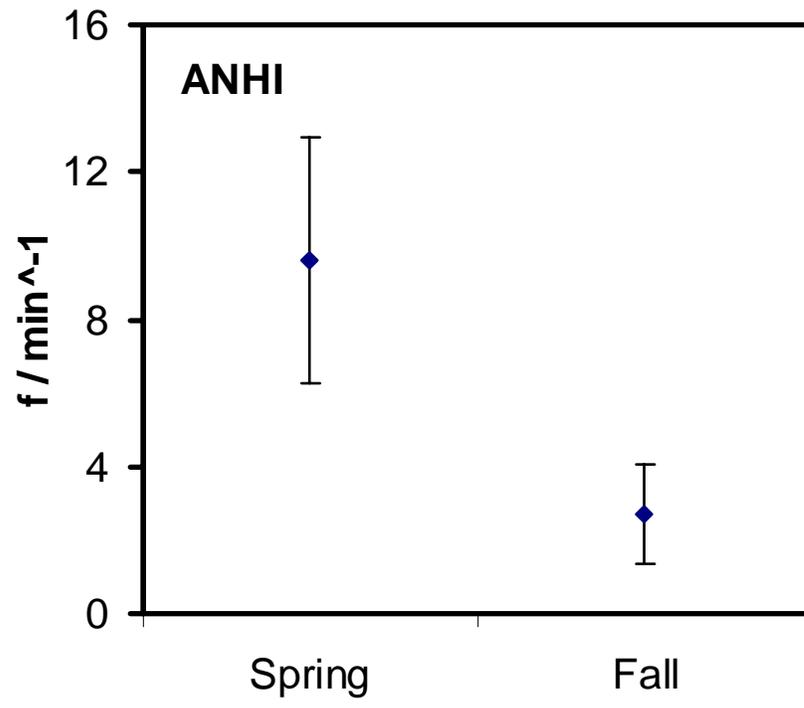
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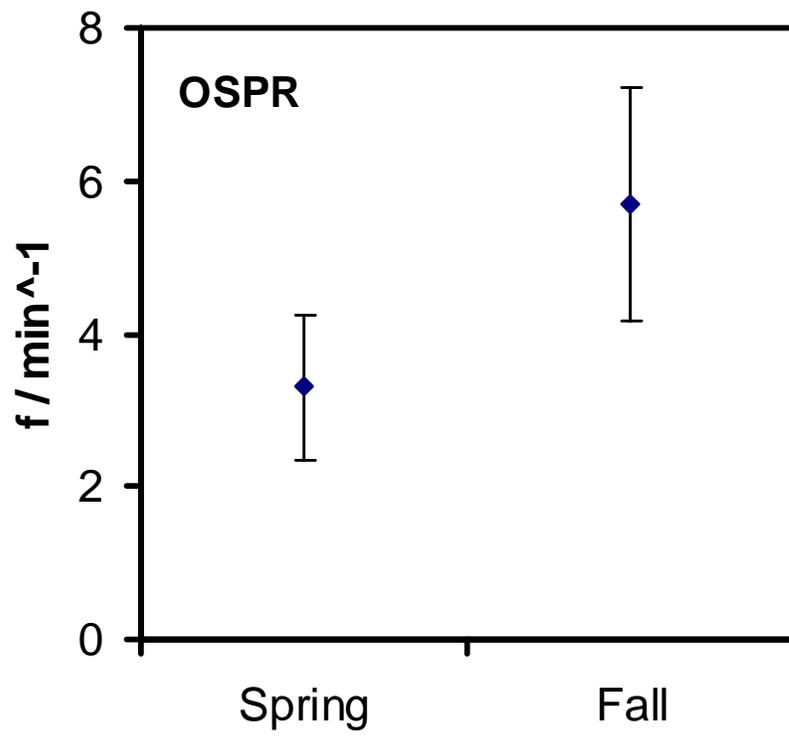
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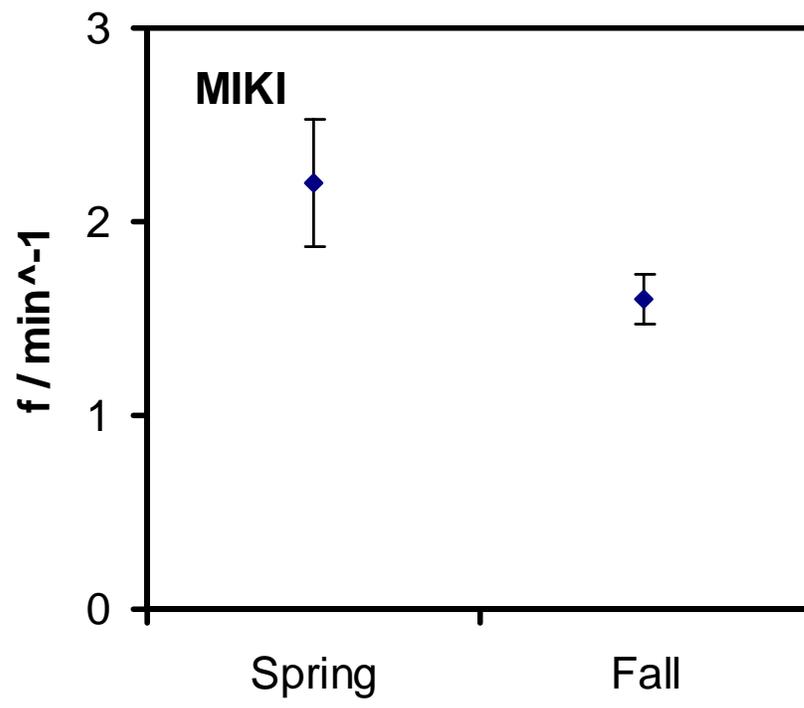
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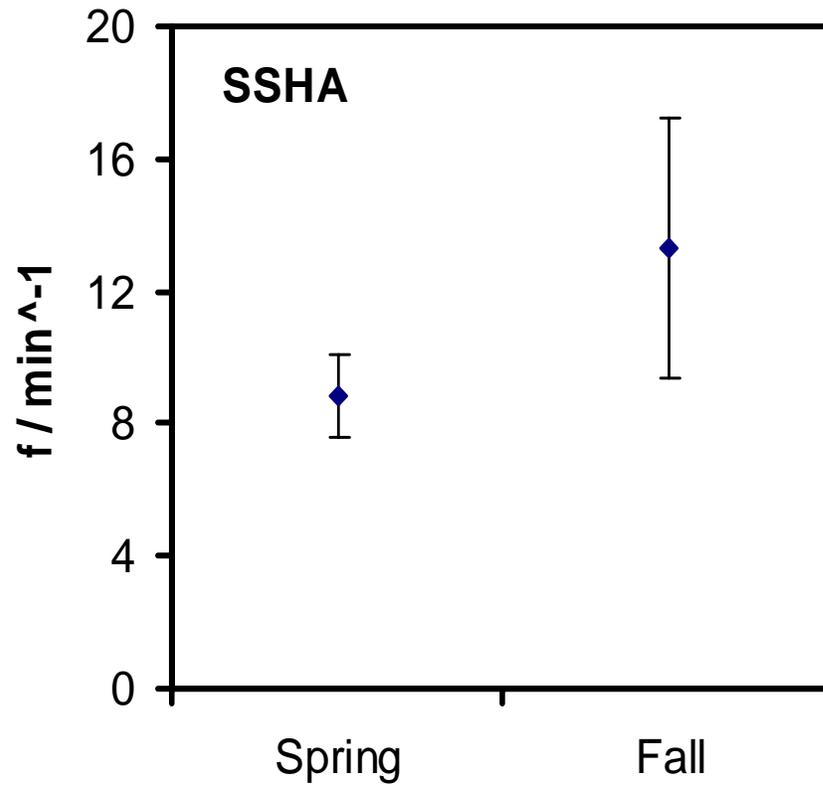
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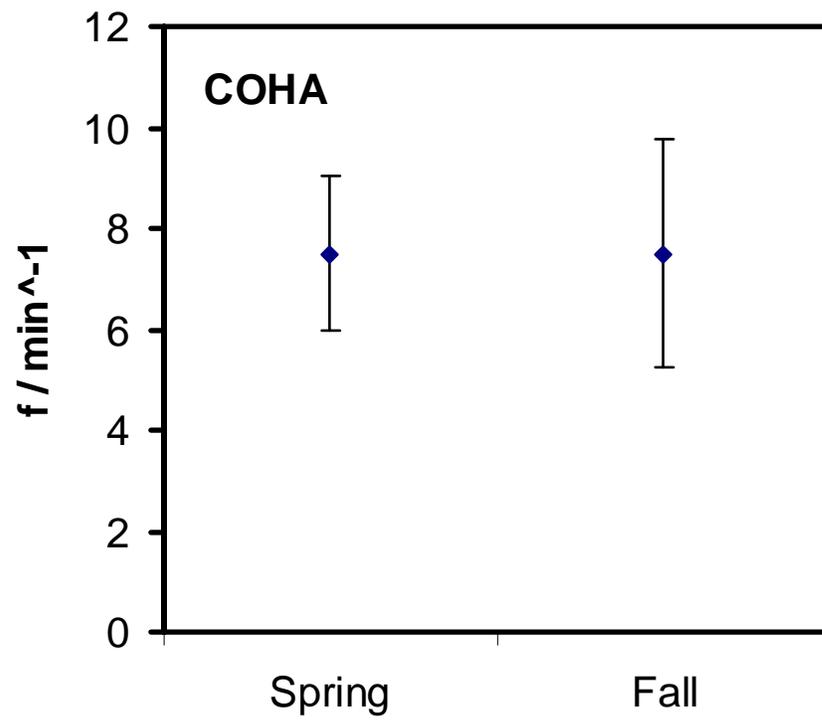
Fig. 1. Wingbeat frequency (f) of nine species of thermal-soaring birds in Veracruz, Mexico, during spring and fall migration (mean, 95% confidence intervals). Acronyms for species are: ANHI=Anhinga, TUVU=Turkey Vulture, OSPR=Osprey, MIKI=Mississippi Kite, SSHA=Sharp-shinned Hawk, COHA=Cooper's Hawk, BWHA=Broad-winged Hawk, SWHA=Swainson's Hawk, and AMKE=American Kestrel.

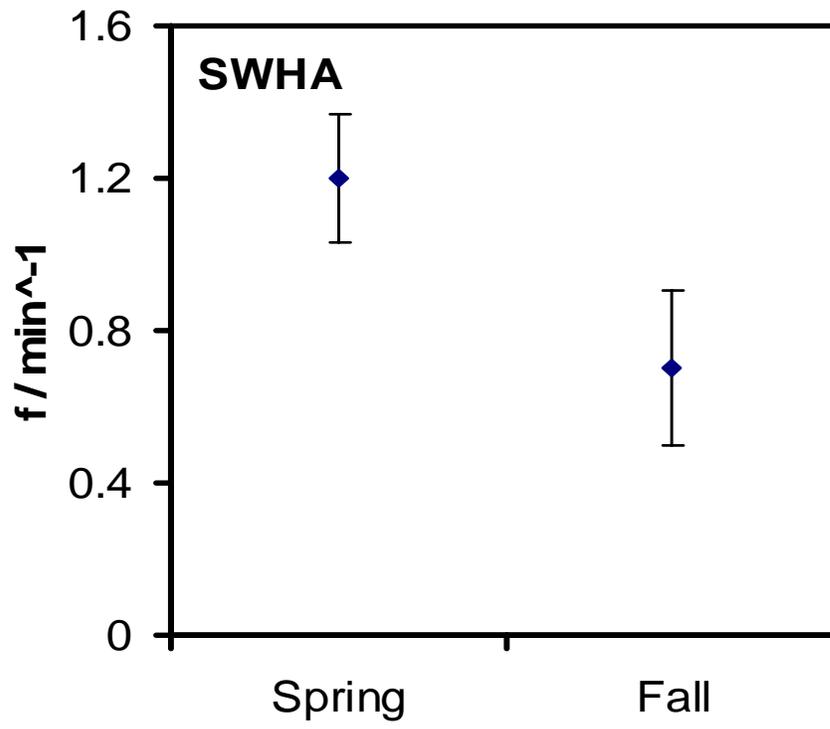


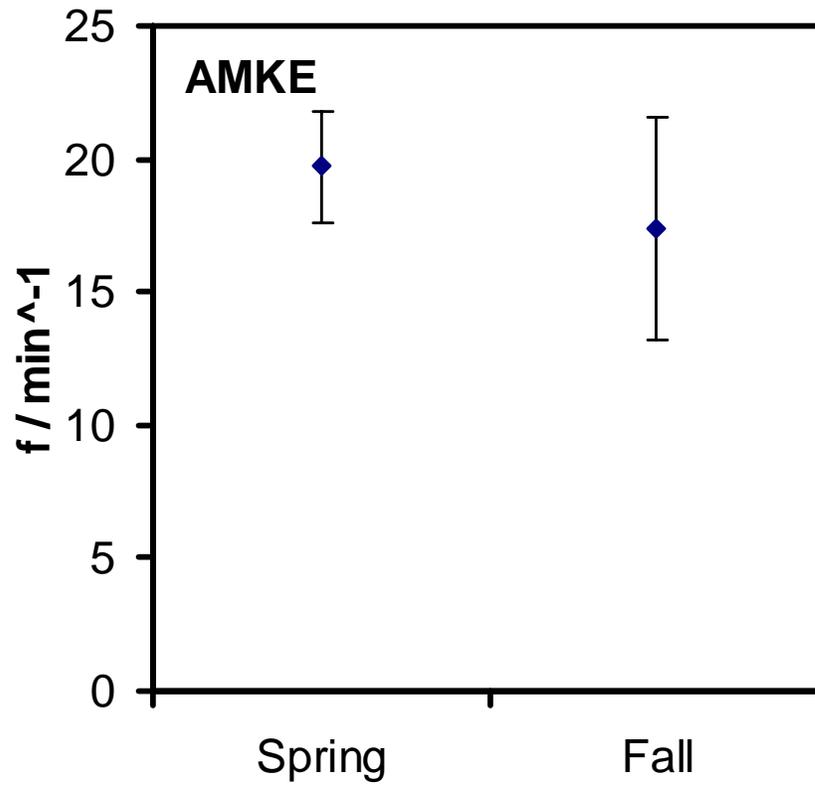


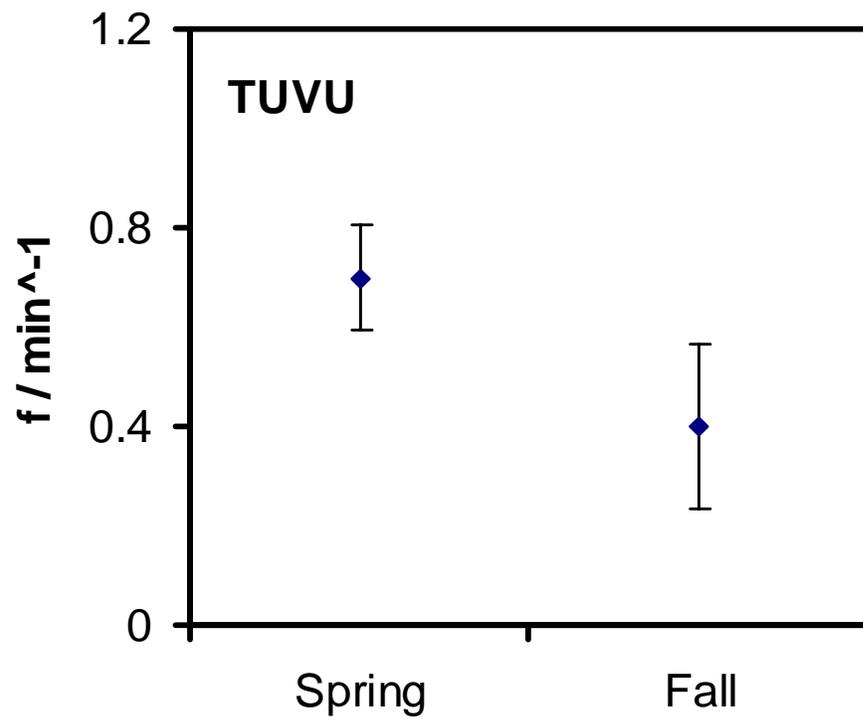


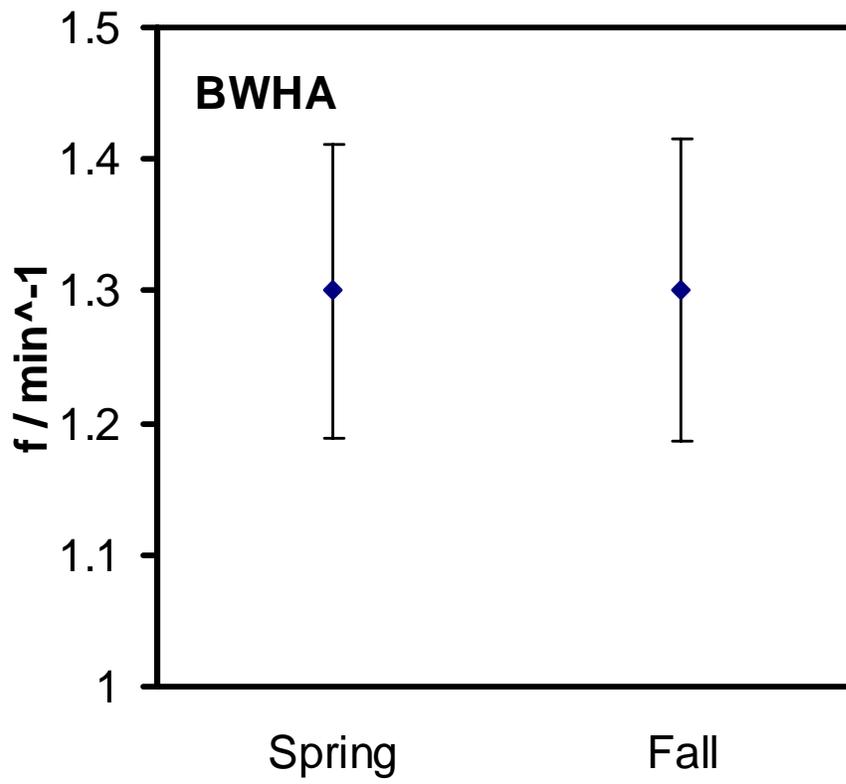












CHAPTER 4

TRENDS IN RAPTOR AND VULTURE POPULATIONS DERIVED FROM MIGRATION COUNTS IN VERACRUZ, MEXICO, 1993-2004

Abstract.- Migration counts of New World vultures and diurnal raptors are a valid technique to assess population trends. Counts from central Veracruz, Mexico, can provide valuable information for some species that are not monitored elsewhere and these counts can cover populations that range from regional to continental scale.

My objectives in this chapter are to evaluate the use of migration counts to monitor populations and to obtain annual estimates of population change for five species over a 10-year period. Here I present the assumptions for these trend analyses and document the rationale behind each step of the method selected. With pooled fall migration data from two sites located at a geographic bottleneck for migrants, I calculated an annual population index and fitted a second-order polynomial regression line to the population index to determine trends and annual estimates of change.

In five species that met both an a priori accuracy target goal and the assumptions of this method, I found significant population increases. The populations of Turkey Vulture (*Cathartes aura*), Osprey (*Pandion haliaetus*), Cooper's Hawk (*Accipiter cooperii*), Broad-winged Hawk (*Buteo platypterus*), and Swainson's Hawk (*Buteo swainsoni*) have been increasing at a rate between +1.6 and +11.1% year⁻¹ and a mean

cumulative increase of 26% between 1993-2004. I was unable to assess population trends in 28 species that had: (1) Very high coefficient of variation in annual counts; (2) Less than 100 individuals recorded per field season (or most individuals distributed in very few days per season); and (3) Shorter coverage of migration period (<75% of the total migration window).

My results have some correspondence with regional and continent-wide trend analyses derived from migration counts elsewhere and to Breeding Bird Survey data from different regions. Because specific information on the geographic origin of migrants recorded in Veracruz is limited and because the proportion of the populations sampled is not known, these comparisons do not provide a full validation of the technique, but suggest the results are generally in agreement with population trends derived from different sources. Quantifying bias in counts and developing models that incorporate measures of intra- and inter-annual variation may enable population trend assessments on many species that I had to exclude from this analysis.

Key words: Population index, population trend analysis, migration counts, vultures, raptors.

INTRODUCTION

The population status of Neotropical migratory birds has been assessed through several survey programs that range in scale from local to continent-wide and are based on different survey techniques (Bart 2005). Because raptors have low densities and secretive habits, most species have not been properly sampled in these surveys (e.g. Breeding Bird Survey [hereon BBS], Sauer and Droege 1992, Rich et al. 2004). Some regions and species lack adequate coverage, and the overall result is a diffuse picture of their status (Zalles and Bildstein 2000; Faaborg 2002).

Raptor migration counts collected over long-term periods have been used to determine regional population trends (e.g. Hussell 1985, Bednarz et al. 1990, Viverette et al. 1996, Hoffman and Smith 2003). However, data from outside Canada and the United States are scarce or lacks long-term continuity (Kjellén and Ross 2000, Bart 2003).

The geographic location of central Veracruz, Mexico, between the breeding range and the wintering range for several species, can provide some valuable insights into populations that are not monitored elsewhere. Moreover, the high proportion of the total population for some species such as Mississippi Kite (*Ictinia mississippiensis*), Broad-winged Hawk (*Buteo platypterus*) and Swainson's Hawk (*Buteo swainsoni*) this single location can provide information on the global population of each species (Appendix 1).

My objectives in this chapter are (1) To evaluate the use of New World vulture and diurnal raptor migration counts from Veracruz to determine population trends; (2) To present adjustments made to a recently-developed methodology for population trend analysis to fit the characteristics of my data set; (3) To calculate the power to detect

population trends at a pre-set accuracy target; and (4) To determine population trends of five species over an 10-year period.

ASSUMPTIONS AND RATIONALE OF ANALYSES

Under ideal conditions, count totals would be an appropriate estimate of variation that could be regressed against time to determine population trends. However, raptor migration counts are highly variable and tend to have skewed distributions, with a few days with many individuals and many days with fewer individuals (Hussell and Brown 1992).

Before doing population trend analyses (Methods section), I present the basic assumptions of this particular case study and justify the method selected. My first assumption is that counts are a sample of the population migrating through central Veracruz, with two independent replicates (with no overlap in counts) of the same population due to having two sample locations. Counts done on a given day are assumed to include different migrants than those counted on any other day. Following this logic, I pooled the data I obtained from both localities into a single measure of the migration (Francis and Hussell 1998).

Secondly, I assume this sample includes a constant or nearly constant proportion of the population over time (Alerstam 1978). Several studies have criticized this assumption, because there are many sources of variation in migration counts besides population change. These sources of variation include: (a) Local and range-wide weather variables (Chapter 2, Kerlinger and Moore 1989); (b) Different timing of migration among years (and annual survey dates may cover a different proportion of the sampled

population (Chapter 2); (c) Observer biases (Satler and Bart 1984); (c) Problems of detection, identification, and estimation (Kerlinger 1989); and (d) Habitat changes around raptor migration count sites (Dunn 2005). However, Bart et al. (2004) and Dunn (2005) argue that accurate quantifications of these effects can be built into models and that adequate sampling design can distribute this error homogenously.

Magnitude of migration is another source of variation. Counts of species with few individuals recorded per season are inherently more variable than migrants recorded in large numbers (Chapter 1). This is reflected in high coefficients of variation (CV) in species of higher rarity, which is unlikely to be a true measure of population size. Abundant birds are expected to have more robust population estimates of because they have lower inter-annual variation.

There have been several different approaches to determine population trends over time using migration counts (Hussell 1981, Fuller and Mosher 1981, 1987, Bednarz and Kerlinger 1989, Hill and Hagan 1991, Ballard et al. 2004). Over the long-term, populations have fluctuations that make population indices oscillate above or below the mean, e.g. over a 25-year period, a population may have a population index decrease followed by an increase, and then followed by a second decrease. A simple linear estimate of population change would therefore not be a good fit for the observed data (Link and Sauer 1997).

In order to circumvent these problems, Hussell (1981, 1985), Francis and Hussell (1998), and Farmer et al. (unpublished ms.) devised a method that includes considerations for these sources of error. This method includes the calculation of a population index that reduces the amount of variation by a series of data manipulations

and transformations, and makes these indices comparable across years. This method estimates change over time through a re-parameterized polynomial regression model that provides a better fit for population index fluctuations over long time series. Population trend estimations following this procedure provide a more realistic outcome that is described in more detail in the Methods section.

Statistical power (the ability to detect a change in a parameter of interest, given that a change exists) entered the discussion of population trend analysis when researchers acknowledged the relationships between variation in counts and survey effort in detecting trends, and decided to include them into ‘target estimation goals’. Butcher et al. (1990, 1993) proposed a ‘reasonable accuracy target’ for detecting population trends in Christmas Bird Counts. This goal has been used as a starting point in subsequent discussions and has been applied to other survey methods, including migration count data (Bart et al. 2004). In this analysis, I follow the accuracy target goal set by Lewis and Gould (2000) for raptor migration counts. My a priori monitoring goal is a data set with the ability to detect a 50% population change over 25 years, with $\alpha=0.10$ and $\beta=0.20$. This approach has been tested in data sets from six different sites and I consider it a reasonable target (Lewis and Gould 2000).

METHODS

Locations, seasons, and dates of study.- The central region of the state of Veracruz, Mexico, lies at the intersection of two major mountainous systems, the Sierra Madre Oriental and the Central Volcanic Belt, which constrain the width of the Gulf coastal plain at about 19° N, ca. 30 km north of Veracruz City. The foothills of the Cofre de

Perote volcano (4,250 m above the sea level, hereon mASL) continue east along the Sierra de Manuel Díaz, to reach the Gulf of Mexico at the vicinity of the fishing village of Villa Rica. This reduction in the course of the Gulf lowland coastal plain forms a geographic bottleneck that funnels spring and fall migrations (Chapter 1, Ruelas 1992, and Ruelas et al. 2000, 2005).

I made counts during spring and fall migrations. Several characteristics of spring migration made this data set useful to describe and quantify migration dynamics, but because of its diffuse patterns, I discontinued its long-term collection (Chapters 1 and 2).

I made these population trend analyses using fall count data from Cardel (19°22'N- 96°22'W, elevation 29 meters above sea level [hereon mASL]) and Chichicaxtle (19°21'N- 96°28'W, elevation 120 mASL), two sites located along a west to east survey line that runs perpendicular to the migration direction (Chapter 1).

Migration counts.- I manned each of these two sites with a team of two field biologists and one assistant that collected hourly migration counts and weather data with hand instruments. From atop vantage observation points (a six-story building in Cardel and a metal tower above tree height in Chichicaxtle), my teams and I identified and counted the total number of migrant raptors, vultures, and wading birds.

We used 8-10x binoculars to scan and identify migrants and 20x Kowa TSN telescopes mounted on sturdy tripods to aid identification. We made counts daily from ~8:00 through 18:00 hrs. CDT, using a modified version of the standard protocol of the Hawk Migration Association of North America (Kerlinger 1989; HMANA 2005). The standard duration of a migration season was 93 days, from 20 August through 20 November of 1993, 1995, 1996, 1998-2004 (n=10 field seasons). Data from 1992, 1994,

and 1997 are excluded from the analysis because of irregular coverage that prevented inter-annual comparisons (Chapters 1 and 2).

Data analysis.- Although the use of migration counts has been validated several times as a valuable tool to assess population trends (Dunne and Sutton 1986), my data set is quantitatively and qualitatively different than migration count data from other localities along leading or diversion lines (fide Mueller and Berger 1967, Farmer et al. unpublished ms.). It includes: (1) A different set of species (some of which were not known to migrate, e.g. the Hook-billed Kite [*Chondohierax uncinatus*], Ruelas et al. 2002); (2) A migration of a different magnitude (>5.1 million birds per season, Chapter 1); (3) A different set of weather conditions; and (4) The potential to have the total population pass by monitoring sites.

Calculation of an annual population index and adjustments to current methods.- I follow the methodology of Farmer et al. (unpublished ms.)

(1) Migration count data from both sites were combined. I calculated the number of birds per day and adjusted these for day of field effort, these weighted values exclude days with < 7 hrs. of observation per day, and days when no data were collected due to adverse weather or other reasons.

(2) Using the PROC UNIVARIATE program of SAS (version 9.1, SAS Institute 2004), I determined the seasonal migration ‘window’ for each season and species separately. The seasonal migration window is the central period during which 95% of the birds pass through my study area, which means the early and late tails of the distribution (with 2.5% of the count) were eliminated.

(3) On a series of dummy variables for date and year interactions, I ran a multiple regression where the predictor variables are dummy values for date and year and the dependent variable is $\ln+1$ of daily counts.

(4) I calculated a regression estimate of the annual population index for the reference year (in log-transformed scale) and calculated indices for years other than the median year of the time series. These regressions produced annual population indices based on log-transformed data, which helps to reduce the distorting effects of a few days in the season when there are exceptionally large numbers of birds. These values were back-transformed into the original scale that represent real bird numbers. There are many measures of central tendency that can be used in these analyses, but Farmer et al.

(unpublished ms.) found that the effort-weighted geometric mean (of passage rate/day) is the metric that performs better. The annual percentage of change is the coefficient of the year variable multiplied by 100. This dependent variable is referred to in Fig. 1 as “Population Index.” Unlike Farmer et al. (unpublished ms.), who used hourly-weighted data in their analyses; I used daily count totals weighted by hourly effort to calculate my population indices (Dunn and Hussell unpublished ms.).

Trends in annual population indices.- Following the recommendations of Farmer et al. (unpublished ms.), I calculated trends by fitting a second-order polynomial regression model to the 10-year time series of population indices (PROC REG of SAS).

In analyzing my data, I left out weather considerations, which are known to affect the number of birds present on a given day. Any long-term trends in weather patterns could cause a change in bird numbers that is not related to true population change, but I

found no published reference that has successfully integrated the effect of these variables into population trend analysis and produced better estimates as a result of its inclusion.

RESULTS

Evaluation of Veracruz migration counts for population trend analysis.- Based on count totals and annual estimates of variation (from Chapter 1), I eliminated many species from the analysis. Nine locally rare species in which the migration window had an average annual total of <100 birds detected or that were found in less than 5 days per season, were not included in this analysis (criteria modified from Dunn and Hussell unpublished ms.). These are White-tailed Kite (*Elanus leucurus*, mean $n=0.7$, CV=150%), Plumbeous Kite (*Ictinia plumbea*, mean $n=4.1$, CV=148%), Bald Eagle (*Haliaeetus leucocephalus*, mean $n=0.1$, CV=0.33), Gray Hawk (*Asturina nitida*, mean $n=180$, CV=142%), Common Black Hawk (*Buteogallus anthracinus*, mean $n=2.1$, CV 177%), Harris's Hawk (*Parabuteo unicinctus*, mean $n=6.9$, CV=54%), Red-shouldered Hawk (*Buteo lineatus*, mean $n=10.1$, CV=73%), Ferruginous Hawk (*Buteo regalis*, mean $n=0.6$, CV=130), and Golden Eagle (*Aquila chrysaetos*, mean $n=0.8$, CV=167%).

I also excluded species for which counts included less than 75% of the days in the species' migration window (Chapter 2, Table 1) or whose counts had a CV higher than 50%, since at present (10-year data set), no coverage is warranted for these species under my model and power assumptions (Hussell 1985, Lewis and Gould 2000). These species are Hook-billed Kite, Swallow-tailed Kite (*Elanoides forficatus*), Mississippi Kite, Northern Harrier (*Circus cyaneus*), Sharp-shinned Hawk (*Accipiter striatus*), Zone-tailed Hawk (*Buteo albonotatus*), Red-tailed Hawk (*Buteo jamaicensis*), American Kestrel

(*Falco sparverius*), Merlin (*Falco columbarius*), and Peregrine Falcon (*Falco peregrinus*).

Population trends 1993-2004.- Five species met the target estimation goals of this analysis and the power estimate per species is presented in Table 1. The population index in use, the effort-weighted Geometric Mean passage rate per day (Farmer et al. unpublished ms.) show population increases in all species (mean= 26.8%) for the period 1993-2004. In the commentaries under each species below, I present a brief description of the trends observed and the estimated annual change for the ten-year period (Table 1). All trends are significant at $P < 0.05$.

Turkey Vulture (*Cathartes aura*). There have been steady annual increases across the decade covered in this study (Table 1). The mean annual increase in the population index is $+5.9\% \text{ year}^{-1}$.

Osprey (*Pandion haliaetus*). I found a net increase of $+3.2\% \text{ year}^{-1}$ in the 10-year period of this analysis. Counts between 1993-1998 show a very rapid increase that was followed by a decrease in the period 1999-2004.

Cooper's Hawk (*Accipiter cooperii*). The pattern observed for Ospreys is similar to the one I found for Cooper's Hawk. There is a sharp increase in the period 1993-1998 with a decrease in the period 1999-2004. Even with this later decrease in counts, the net trend is $+1.6\% \text{ year}^{-1}$.

Broad-winged Hawk. I found a steady, net positive trend in the 10-years of this study (+2.9% year⁻¹). This is the weakest trend estimate of all the species, with a trend line influenced by the low number of birds estimated in 1993 and the lack of coverage in 1994.

Swainson's Hawk. This species has the highest net increase in the 10-year period of study (Table 1). During the period 1993-1995 there was a net increase followed by a decline in the years 1996-1998 and a second period of increase after 1999 that continues to this date. The net population trend is +11.1% year.⁻¹

In all the trends shown, population indices are low in the 1993 season. It is possible that values collected in this field season are more biased than in subsequent years because of field crew expertise. Although field crews started working in this project in 1991 and most of the field biologists in the team had at least two seasons of field experience, it is possible that 1993 values are more conservative estimates different from those of other years. These lower values have an influence in the trend detected for the 10-year period.

DISCUSSION

This evaluation of migration count data for one species of New World Vulture and 23 species of diurnal raptors omits most species from the trend analysis because these species have high yearly variation in counts, which results in low power to meet target estimation goals. After some adjustments to a recently developed methodology and

calculations of power, I was able to analyze trends for five species, all of which had positive, significant trends over the 10-year period 1993-2004.

Value of Veracruz migration counts to determine population trends.- The geographic location of central Veracruz in relation to breeding and wintering ranges of species, and the large proportion of their global population that migrates through this region (Appendix 1), provides a unique opportunity to monitor population trends from a single location. However, obtaining information from localities with large quantities of migrants can be challenging. I have identified the following sources of error in migration counts: (a) Detection (e.g. small birds are more difficult to detect than large birds, species that migrate alone are more difficult to detect than species that migrate in large flocks); (b) Identification (nearly 2% of the migrants are not positively identified, >100,000 birds per season); and (c) Quantification of large numbers of migrants (errors in estimation have a positive relationship with flock size).

Adjustments to deal with these sources of error have been suggested by Bart et al. (2004). They recommend quantifying the sources of error, e.g. observer quantification bias, and incorporate this source of variation to trend calculations. For example, if observer bias (b) is estimated as $\pm 1\%$ of the count, the upper and lower limits of this error can be deducted/added to zero (bias is assumed to be zero in power estimations). With this, we can obtain a lower and upper estimate of bias, $b_l = -0.01$ and $b_u = 0.01$. If the estimated rate of change is 1, we can only conclude there has been change if the estimated value is $1 + b_u$ or $1 - b_l$. Inclusion of several sources of error is possible and they have developed an equation to incorporate these biases (Bart et al. 2004). I have not quantified sources of error in Veracruz counts, but it would be worth attempting to adjust

data for estimated bias and reduce the number of species left out of the analysis. This would allow us to include rare species (those with <100 individuals per season) in the analysis.

Power and ability to meet target estimation goals.- Species with high inter-annual variation require longer time series to detect significant trends, because power of these assessments decreases as CV increases (Butcher 1990, 1993; Lewis and Gould 2000). Power analysis can help us to determine the length of the time series needed to detect trends in species with a high CV (Bart et al. 2004). One of the drawbacks of this method of power calculation is that has been found to perform better estimating positive than negative trends (Lewis and Gould 2000).

Validation of population trend estimations for species.- I have insufficient information on the origin of migrants recorded in Veracruz and an approximate estimate of the proportion of the population sampled to attempt a quantitative comparison of the trends observed with data from other sources, so the following discussion should be viewed with caution. Yet, I found some correspondence between data from different sources and my results. These data come mostly from BBS, whose limitations with regards to detecting raptors have been presented above. I found very few additional sources of information, and this is mostly anecdotal. These population trend estimations are closely linked to the geographic origin of migrants and the proportion of the population sampled here (Appendix 1).

Turkey Vulture. I assume a highly significant proportion of the North American population migrates through my field sites, but the approximate proportion of the total

North American population can not be assessed from existing estimates (Appendix 1). The annual rate of increase I found (+5.9% year⁻¹ between 1993-2004) is over twice the +2.3 trend observed in survey-wide estimates of the Breeding Bird Survey in the period 1980-2004 (n=2,077 BBS routes) (Sauer et al. 2005). Kirk and Mossman (1998) report the species is expanding rapidly and increasing in numbers, although they make no quantitative estimations. Christmas Bird Count data also show increases in the United States and Canada in the period 1993-2004 (from 0.59 – 0.64 per party/hour) (National Audubon Society 2005).

Osprey. The proportion of the global population of this species that migrates through Veracruz is marginal (Appendix 1) and these birds seem to come from very different localities (Martell et al. 2001; Elliot et al. unpublished ms.) so it will be difficult to find adequate correspondence between migration and breeding range data from a specific region. Osprey is experiencing significant increases across its range (Poole et al. 2002). Recently, Hoffman and Smith (2003) report increases in six migration monitoring sites in western United States in the period 1977-2001, and Farmer et al. (unpublished ms.) report increases of 1.6-2.8% year⁻¹ in Pennsylvania and New Jersey in the period 1976-2003. Sauer et al. (2005) report a range-wide annual increase of 5.1%, based on 412 BBS routes in the period 1980-2004. This is an increase higher than the net +3.2% for the 10-year period reported here. There is no published information about recent declines that matches the one reported here.

Cooper's Hawk. This is another species that is marginally recorded in Veracruz (Appendix 1), and for which there exists little information on geographic origin. A few unpublished band recoveries from a banding station in Veracruz (Scheuermann and Ruelas 2003), indicate these hawks come from the upper Midwest, and it is reasonable to believe most of the migrants we track in Veracruz come from the Central Flyway. Mexican band recoveries of hawks banded in several migration monitoring sites in W United States indicate Cooper's Hawks recorded in Veracruz do not come from the Rocky Mountain or Intermountain Flyways (Hoffman and Smith 2003).

The Cooper's Hawk is a species difficult to detect in BBS routes. Data from 64 routes from the Central BBS Region between 1980-2004 report a +7.8 annual increase in the period 1980-2004, over three times the +1.6% year⁻¹ value reported here.

Broad-winged Hawk. A substantial proportion of the global population of this species funnels through Veracruz in spring and fall (Appendix 1), therefore a range-wide comparison of trends is reasonable. I found +2.9% year⁻¹ in migration counts from Veracruz that contrast with a net decrease of -0.1 found in 656 BBS routes, although this value is not statistically significant (Sauer et al. 2005). Data from migration monitoring sites elsewhere is in closer agreement with BBS data than values I found in Veracruz. Farmer et al. (unpublished ms.) found a net decrease of -3.0% year⁻¹ in Pennsylvania and -1.1% year⁻¹ in New Jersey. In an earlier period, Titus and Fuller (1990) report possible regional shifts in Broad-winged Hawk distribution that may be influencing trends observed in eastern sites. Hoffman and Smith (2003) found disparate results (a mix of increases and stable trends) in six sites in western United States. Lower population

estimations in the early period of my investigation also influence the overall trend, which could be less pronounced than the increase I report here.

Swainson's Hawk. A very high proportion of the global population of this species migrates through Veracruz (Appendix 1) and it is also reasonable to make range-wide comparisons of population trends with the values found in Veracruz. Using data from six migration monitoring sites in the western United States, Hoffman and Smith (2003) estimate stable to increasing trends in most of their sites, which is in agreement with my results. However, Sauer et al. (2005) report significant decreases in survey-wide BBS (-1.01% year), based on 650 BBS routes in the period 1980-2004. The negative trends observed in data from Veracruz in the mid 1990s and subsequent recovery coincides with incidents of massive mortality in Argentina reported by Woodbridge et al. (1995).

In summary, my research shows that we can use counts from Veracruz to determine population trends for some species that meet the assumptions of currently existing methods. One important step in improving our capabilities to determine population trends for more species, is the ability to quantify different sources of bias and incorporate these estimates into new models for population trend analysis. Obtaining more detailed information on geographic origin of the migrants can help to validate the trends reported by comparing them to other surveys that cover these species (James and McCulloch 1995).

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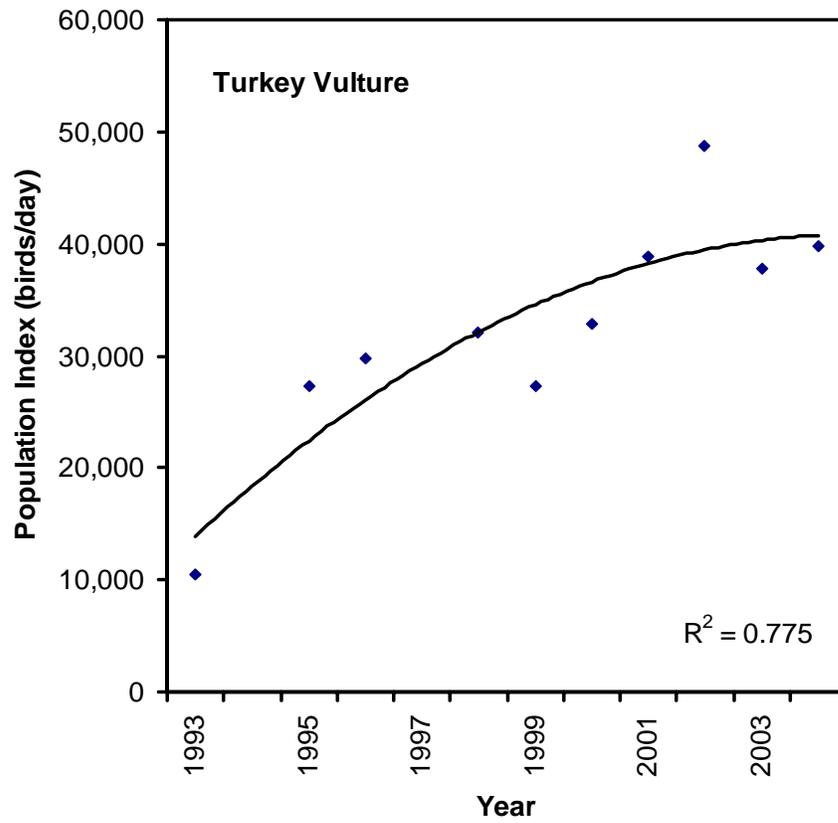
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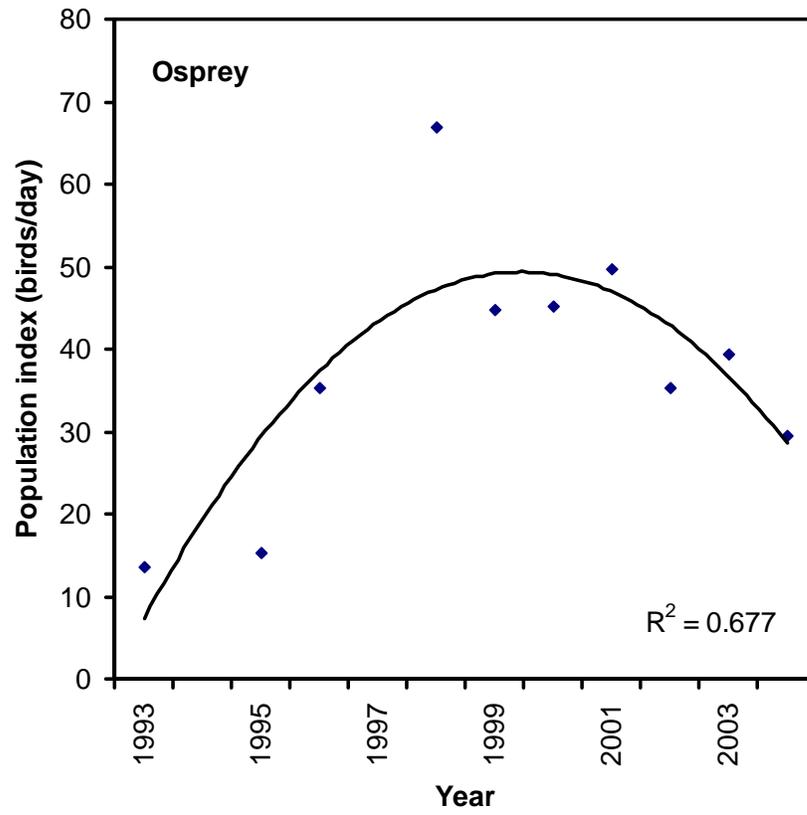
Table 1. List of species recorded in migration counts in Veracruz, Mexico. The mean number recorded excludes the field seasons of 1994 and 1997. Standard error and coefficient of variation are given as a mean to interpret variation in counts among years. Species marked with an asterisk are those with higher potentials for trend estimates of appropriate power sensu Lewis and Gould (2000).

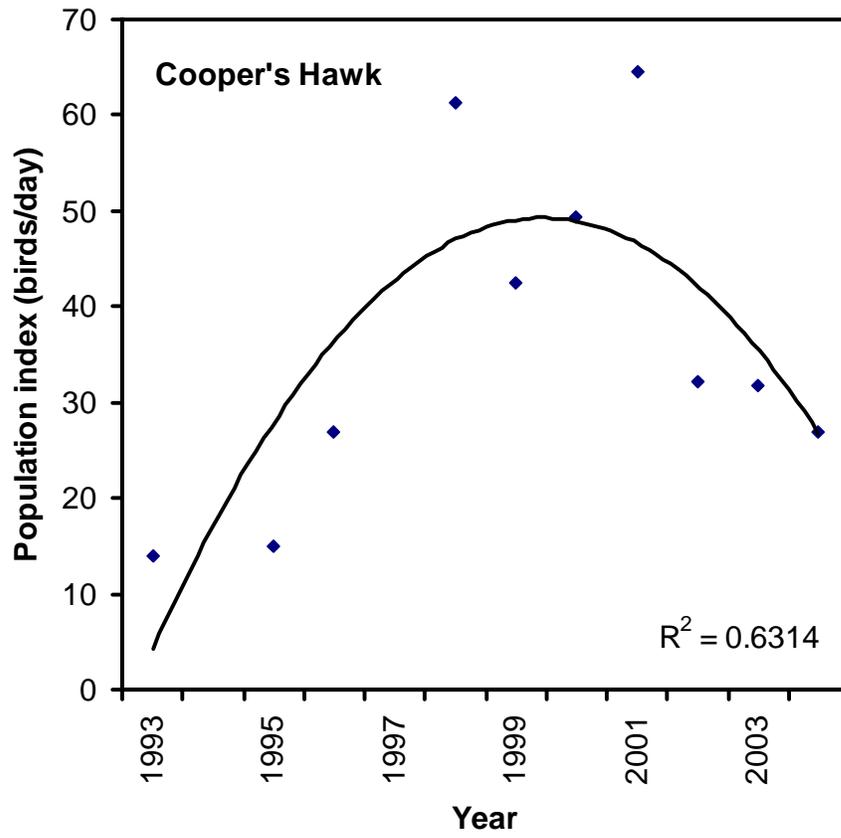
	Mean n counted during 95% migration window	SD (\pm)	CV(%)	Annual % change
Turkey Vulture	1,752,865	548,912	31.3	5.9
Osprey	2,809	1,192	42.4	3.2
Cooper's Hawk	2,260	1,095	48.4	1.6
Broad-winged Hawk	1,818,042	422,675	23.2	2.9
Swainson's Hawk	715,020	331,722	46.4	11.1

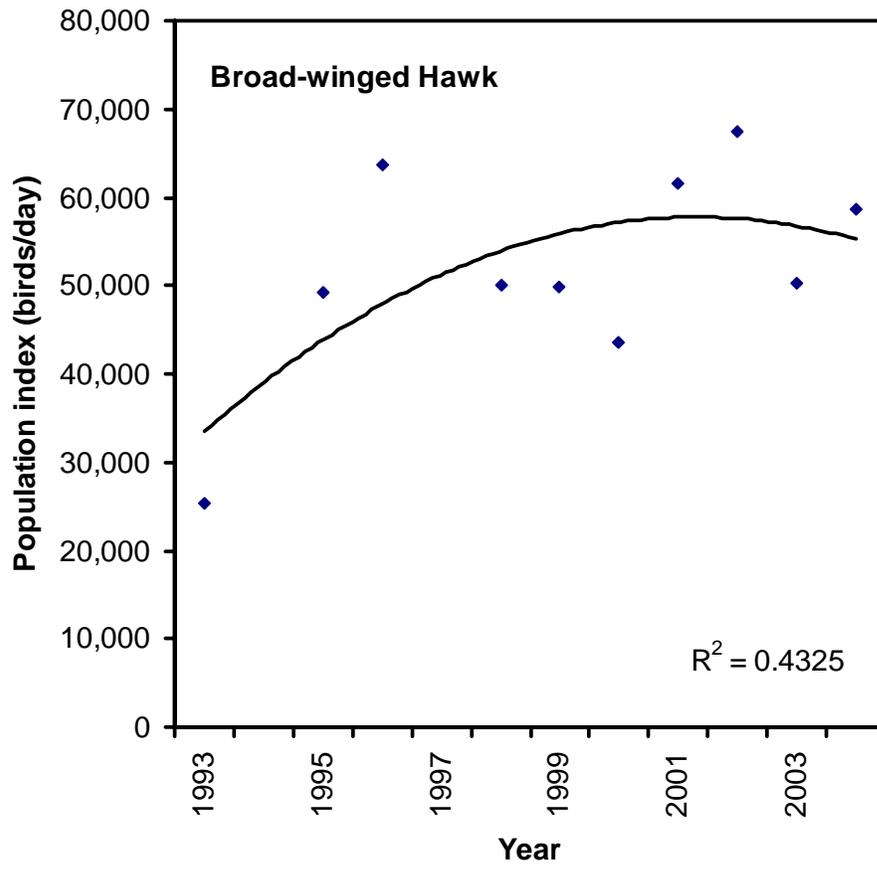
FIGURE LEGENDS

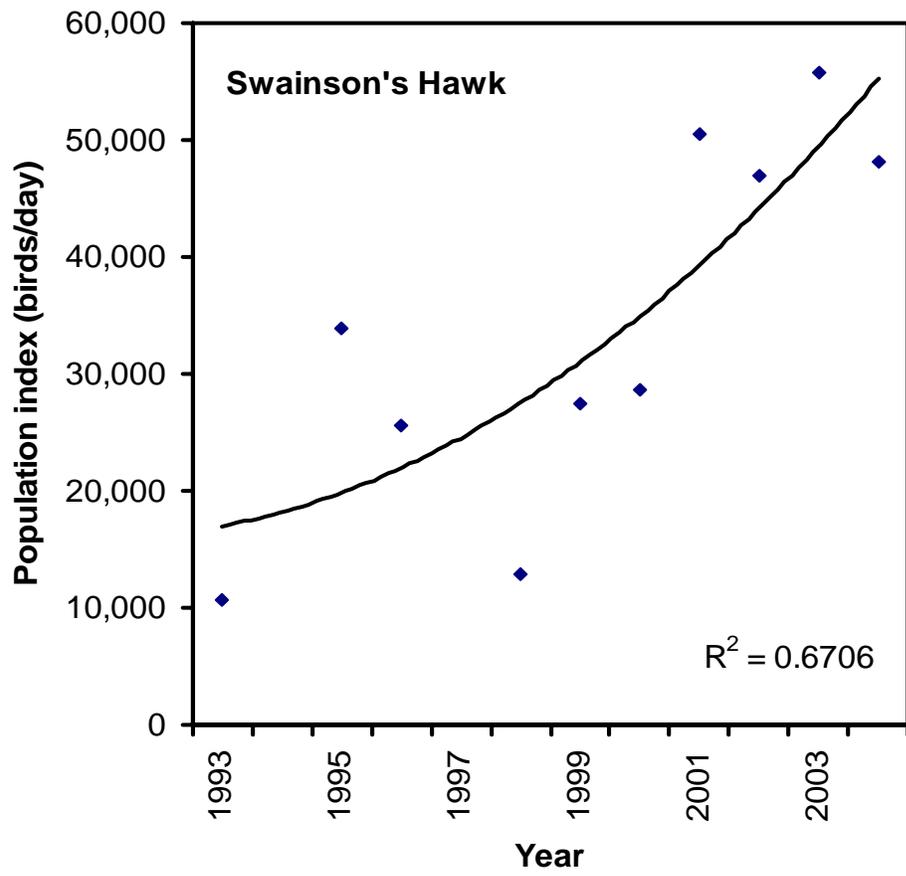
Figure 1. Trends in the populations of one species of New World Vulture and five species of diurnal raptors derived from migration counts in Veracruz, Mexico, 1993-2004.











APPENDIX 1

NORTH AMERICAN POPULATION ESTIMATES FOR 33 SPECIES OF MIGRANT BIRDS AND THE RELATIVE IMPORTANCE OF A STOPOVER SITE IN VERACRUZ, MEXICO

Here I present North American population estimates for 33 species of wading birds, vultures, and diurnal raptors covered in my dissertation. I also include an approximation of the proportion of each population that migrates through Veracruz, Mexico, based on range maps in Birds of North America species accounts and recent North American population estimations.

Most wading bird species estimates are originated from colony counts and aerial surveys, while those of raptors are from Breeding Bird Survey, road surveys, and migration counts. Population estimates have recently been revised by Kushlan et al. (2002) and Rich et al. (2004). No asterisk after the name means the species is only marginally present in the area or I believe my study sites only sample a modest (<1%) of the total population (n=18 species); (*) denotes 2-10% of the estimated North American population is recorded migrating through this region (n=7 species); and (**) denotes between 11-99% (??) of the North American population is recorded in Veracruz (n=8 species). In three species of migrants, these proportions may be >95% of the North American population.

Based on my arguments on the accuracy of my count data (see Chapter 1), I suggest revising the North American population estimates in seven species where these data are lower than my count data. Three species marked with (†) are range extensions.

American White Pelican (*Pelecanus erythrorhynchos*).** Globally estimated between 106,690 (53,345 nests x 2 *fide* Koonz 1987) and 120,000 individuals (Kushlan et al. 2002). Highest Veracruz count (fall 2002) is 7.29% higher than previous global estimates. Since the majority of the winter range for his species lies N of my study sites (Knopf 2004), I believe that either the known winter range and/or the North American population estimates need to be revised.

Neotropic and Double-crested Cormorants (*Phalacrocorax brasilianus* and *P. auritus*). These species are not recorded in significant numbers, cormorants may follow an entirely coastal migration path and over water migration (Telfair and Morrison 1995, Hatch and Weseloh 1999).

Anhinga (*Anhinga anhinga*).** Current North American population estimates range between 20,000-34,000 individuals (10,000-17,000 pairs x 2 *fide* Frederick and Siegel-Causey 2000, Kushlan et al. 2002). My highest fall count (fall 2002) is 21.88% larger than this estimate. Population estimates should be revised.

Great Blue Heron (*Ardea herodias*).* Population estimates are 83,000 (Kushlan et al. 2002) and the highest count (fall 1998) represents 2.61% of this total. This is a conspicuous species that is either marginally present during migration at my study sites or the species may have nocturnal/diurnal migration habits (Butler 1992).

White Ibis (*Eudocimus albus*).* Reportedly the most numerous wading bird along its range (Kushlan and Bildstein 1992), its North American population is estimated at 100,000 individuals (Kushlan et al. 2002), most of them from Florida. The highest number recorded (fall 2004) is 4.69% of this total.

White-faced Ibis (*Plegadis chihi*).* Also estimated to be 100,000 birds in North America (Ryder and Manry 1994, Kushlan et al 2002). The highest count from Veracruz is 3.87% of this total (fall 2002). This may be a migrant whose migration flyway is not restricted to the coast.

Jabiru (*Jabiru mycteria*). The Kushlan et al. (2002) estimate for North America is 450 individuals. I suspect my birds originate in S Mexico, (the Grijalva-Usumacinta area or the wetlands of Centla, Tabasco) and disperse N after the breeding season (see comments under following species).

Wood Stork (*Mycteria americana*).** This species is estimated to have 25,000 individuals in the United States breeding range (Coulter et al. 1999) and a more recent North American population estimate of 46,000 individuals includes Mexico and Central America (Kushlan et al. 2002). The average number recorded in Veracruz is higher than both of these estimates, and largest number recorded in Veracruz (fall 2002) is 164.76% larger than any of them. These results suggest population estimates should be revised. Wood Storks recorded in Veracruz may be juveniles dispersing N from wetlands in the Grijalva-Usumacinta rivers and the region of Centla and the number of individuals

recorded in migration counts may not belong to populations originating in the SE United States.

Turkey Vulture (*Cathartes aura*).** Population estimates cover a broad range (Kirk and Mossman 1998). The United States and Canada population estimate in Rich et al. (2004) is 1,305,000 individuals (29% of 4,500,000). My average annual count is higher, and the largest number recorded (fall 2002) is 5% larger than this quantity. This population estimate should also be revised.

Osprey (*Pandion haliaetus*).* The Canada, United States, and NW Mexico (breeding range) estimates are widely variable, and range from ca. 42,000 (20,800 pairs x 2 fide Poole et al. 2002) to 211,600 (46% of 460,000) (Rich et al. 2004). My highest count (fall 1998) is 2.39% of this total, which suggests Veracruz is only a marginal locality for their migrations.

Hook-billed Kite (*Chondrohierax uncinatus*).** The North American (United States) population estimate is 2,000 individuals (1% of 200,000 fide Rich et al. 2004). My highest count (fall 2000) is 15% of this estimate. I am uncertain about the geographic origin and populations involved in the migrations of these birds, and a careful analysis of their migration is currently under preparation (Ruelas et al. 2002).

Swallow-tailed Kite (*Elanoides forficatus*).* North American population estimates range between 1,600 (800 pairs x 2 fide Meyer 1995) and 7,500 individuals (5% of 150,000, Rich et al. 2004). My highest count (fall 2001) represents 3.81% of these estimates.

White-tailed Kite (*Elanus leucurus*). This species is recorded only marginally in Veracruz (Dunk 1995). I suspect this is an intratropical migrant with partial population withdrawal at the N end of its distribution.

Mississippi Kite (*Ictinia mississippiensis*).** The North American global population estimates by Rich et al. (2004) are based on Parker (1999), who obtained information from my count data. This is a total migrant whose most important migration route is presumably the Gulf coast, and I suspect a high percentage of the global population of this species is tallied in my count sites. The maximum number ever recorded is 306,274 (fall 2002), 61.19% percent higher than my previous estimate from 1998 cited by Parker (1999).

Plumbeous Kite (*I. plumbea*). Marginally recorded, see footnote of Table 2 in Chapter 1.

Bald Eagle (*Haliaeetus leucocephalus*). This species is only marginally recorded (Buehler 2000).

Northern Harrier (*Circus cyaneus*). Estimated to have between 111,000 and 455,000 individuals in North America (MacWhirter and Bildstein 1996, Rich et al. 2004), my highest count (fall 2000) is only 0.18% of the total estimate. My study area is located in the southernmost third of the wintering range.

Sharp-shinned Hawk (*Accipiter striatus*).* The North American population estimate is 583,000 individuals (53% of 1,100,000 fide Rich et al. 2004). The highest count from Veracruz (fall 1998) is only 1.79% of this total. As with the previous species, my study

site is located in the southernmost third of the wintering range (Bildstein and Meyer 2000).

Cooper's Hawk (*A. cooperii*). The only North American population estimate of 552,900 individuals (97% of 570,000 *fide* Rich et al. 2004, Rosenfield and Bielefeldt 1993) means that my maximum count (fall 2001) comprises only 0.72% of the total.

Gray Hawk (*Asturina nitida*), Common Black Hawk (*Buteogallus anthracinus*), and Harris's Hawk (*Parabuteo unicinctus*). These are local/intratropical migrants of uncertain geographic origin (Schnell 1994, Bednarz 1995, Bibles et al. 2002), recorded only marginally in my study sites.

Red-shouldered Hawk (*Buteo lineatus*).⁺ The North American population estimate is 821,700 individuals (99% of 830,000 *fide* Crocoll 1994). Although this species is recorded regularly, my study site is a southern extension of the winter range.

Broad-winged Hawk (*B. platypterus*).^{**} Global population estimates of 1.7 million individuals are based on research from my study site (Goodrich et al. 1996). This estimation is also the basis of the more recent estimate of 1,728,000 individuals (96% of 1,800,000 *fide* Rich et al. 2004). The highest number recorded in Veracruz (fall 2002) is 38.26% larger than the North American estimate, which should be revised. This species is a total migrant (breeding and wintering ranges are disjunct), and I believe that, with the exception of populations overwintering in S Florida and individuals migrating across the Greater Antilles into Cuba, a very large proportion of the global population is recorded during migration at my research sites.

Swainson's Hawk (*B. swainsoni*).** This is another species of total migrant whose global population estimates are based on unpublished data from my research sites (Ruelas et al. 1996). During the period 1995-1996 my estimates ranged from 448,000-845,465 (England et al. 1997), and this figure was used by Rich et al. (2004) for their estimate of around 460,600 (94% of 490,000). The highest number recorded in Veracruz (fall 2003) is 60.40% larger than the previous population estimate, which I suggest should be revised. The migration of this 'western' species follows a path across northern Mexico into the Gulf coastal plain and most of the Swainson's Hawks overwinter in Argentina, with the exception of a few individuals in eastern Oaxaca (Binford 1989) and Florida (England et al. 1997). The disjunct distribution of this species in the breeding and wintering area, and the limited options for migration routes suggest a very large proportion of the global population migrates through this bottleneck (e.g. Fuller et al. 1998).

Zone-tailed Hawk (*B. albonotatus*). This species is only marginally recorded in Veracruz (Johnson et al 2000).

Red-tailed Hawk (*B. jamaicensis*). This species is also marginally recorded (Preston and Beane 1993).

Ferruginous Hawk (*B. regalis*)⁺ and Golden Eagle (*Aquila chrysaetos*)⁺ These species are only marginally recorded (Bechard and Schmutz 1995, Kochert et al. 2002); my observations are the southernmost records of their winter range.

American Kestrel (*Falco sparverius*). Reportedly ‘the most common North American falconiform’ (Smallwood and Bird 2002), its populations have been estimated at 4,350,000 (75% of 5,800,000 fide Rich et al. 2004). The highest number recorded in Veracruz (fall 1998) is only 0.49% of the global estimate. My study sites are located in the northern half of its wintering range (Smallwood and Bird 2002).

Merlin (*F. columbarius*). North American estimates are around 650,000 individuals (50% of the total 1,300,000 estimated to compose the global population size of this Holarctic species, fide Rich et al. 2004). The relatively few records of this species in my migration counts (0.05% of the population estimate) suggest either geographically-widespread or entirely coastal migratory movements (Sodhi et al. 1993). See comments on Merlin as a solitary migrant using powered flight in Chapter 1.

Peregrine Falcon (*F. peregrinus*).* The North American population estimate for this species is highly variable and ranges from 50,000 (White et al. 2002) to 276,000 (23% of the global 1,200,000 of this cosmopolitan species, Rich et al. 2004). The highest number recorded from Veracruz (fall 1998); is a proportion that ranges between 0.53 to 2.93% of these estimates. There are several factors that make my estimation complicated: (1) the wide variation of North American population estimates, (2) the presence of Peregrine Falcons in the winter season throughout most of the breeding range, (3) its coastal migration habits that leaves many migrants in Veracruz unrecorded in migration counts, and (4) well documented water-crossing behavior in the Peregrine Falcon (Kerlinger 1985, White et al. 2002). I believe counts from my study sites cover a very modest proportion of the total North American population.

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APPENDIX 2

VERACRUZ RIVER OF RAPTORS PROJECT FIELD BIOLOGISTS (N=92, >30 HRS
OF FIELD WORK) INVOLVED IN DATA COLLECTION, DATA ENTRY, DATA
PROOF-READING, AND FIELD CREW COORDINATION
(IN ALPHABETIC ORDER, 1991-2004)

Sergio Humberto Aguilar Rodríguez	Hugo Corzo Aguirre
Héctor Alafita Vázquez	Octavio Gerardo Cruz Carretero
Alejandra Alvarado	David Curson
Adriana Álvarez Andrade	Charles D. Duncan
Claudia Álvarez Aquino	Mark Faherty
Ingrid Arias	Laura Fernández
Carlos Armenta Contreras	Christian Fregat
James Locke Barr Olivo	Flor Elena Galán Amaro
Luis Barradas	Julio César Gallardo del Ángel
Corrie Borgman	Juan Manuel García
Yumei Cabrera Carrasco	Jeronimo García Guzmán
Francisco Cano	Alexaldo García Miranda
Héctor Cano	Gregory A. George
Efraín Castillejos Castellanos	Clementina González
Irving Chávez	Korina González Camacho
Liliana Cortés Ortiz	Laurie J. Goodrich

Omar Gordillo Solís	Rigoberto Mendoza Rebolledo
Peter Gustas	Sandra Luz Mesa Ortiz
John Haskell	Brian Mongi
David Heeden	Jorge Ernesto Montejo Díaz
Olivia Hernández	Citlali Guadalupe Morales
Eric Hernández Molina	Eileen Müller Guerra
Stephen W. Hoffman	Russell Namitz
Mark Hopkins	Sean O'Connor
Yedi Juárez López	Jeff Ogburn
Mike Lanzone	Delfina Olivares
Larry LaPré	Gustavo Ramón
Grez Levandoski	Luis Fernando Rincón Ramos
Julio Lobato	Juan Carlos Rodríguez
Héctor López Pale	Rafael Rodríguez Mesa
Juan Marín	Ernesto Ruelas Inzunza
Beatriz Márquez	Karen L. Scheuermann
Alberto Martínez Fernández	Maria de los Ángeles Segura
Eduardo Martínez Leyva	Evodia Silva Rivera
Niels Maumanee	Tim Smart
Jeff Maurer	Zachary N. Smith
Kirsten McDowell	Karlo Antonio Soto Huerta
Nathan McNett	Robert Straub
Jennifer McNicoll	César Tejeda Cruz

Dominic Thiebault

Susan Thomas

Andy Thoms

Jim Tietz

Ruth Tingay

Jeanne R. Tinsman

Ricardo Valenzuela

Liliana Vanda

Rafael Villegas Patraca

Meghan Walker

Scout Weidensaul

Habacuc Ychante Huerta

Carlos Zavala Blas

James R. Zelenak

VITA

Ernesto Ruelas Inzunza was born in Monterrey, Nuevo León, México, on 6 May 1968. He was raised in several different cities in Mexico and settled in Xalapa, Veracruz, at age 11. Ernesto received his B.Sc. in Biology/Terrestrial Ecology from the Universidad Veracruzana in 1991. In that same year, Ernesto and his colleagues Laurie Goodrich and Steve Hoffman founded the Veracruz River of Raptors Project. This is a long-term, collaborative initiative that started in 1991 and has continued to this date. He has done ecological and ornithological research in many locations in Tamaulipas, Veracruz, Chiapas, Oaxaca, and the Yucatan peninsula, Mexico, and in several localities in Guatemala, Costa Rica, Panama, Puerto Rico, and the United States.

In 1994, Ernesto founded a state chapter of the conservation non-profit organization Pronatura. As executive director, his duties in Pronatura Veracruz (PV) centered on conservation and sustainable development projects in the Zoque rainforest, the Alvarado wetlands system, the state's cloud forests, and the River of Raptors. His work included planning, fundraising, and the administration of time, human, and monetary resources as well as the development of work alliances with partners that ranged from grassroots to international conservation organizations.

Ernesto's work in PV continued until August 2001 when he started graduate school. He completed his Ph.D. in Ecology, Evolution, and Behavior, at the Division of

Biological Sciences; and a Geographic Information Systems Graduate Certificate from the Forestry Department, University of Missouri, in November of 2005 (advisor: John Faaborg). He belongs to eight scientific and conservation societies and has participated actively in the organization of meetings, symposia, and academic and conservation networks, and will co-chair the local committee of the forthcoming IV North American Ornithological Conference in Veracruz in October 2006. Ernesto was awarded a Partners in Flight leadership award in 2002. He has taught or has been a teaching assistant for several courses, including General Ecology, Ornithology, Environmental Science, and Tropical Ecology at the Universities of Missouri, Nebraska, and Universidad Veracruzana.

His current research interests are the spatial and temporal dynamics of raptor and wading bird migration and monitoring applications of long-term data sets derived from migration monitoring projects. At present, Ernesto works as Raptor Population Index (RPI) Project Manager. RPI is a partnership of the Hawk Migration Association of North America, Hawk Mountain Sanctuary, and HawkWatch International and is housed at the Cornell Lab of Ornithology in Ithaca, NY. The goal of RPI is to contribute to the effective conservation of raptors through migration monitoring, assessments of population status, and the generation of information for educational and conservation purposes.