SEASONAL ABUNDANCES AND DISTRIBUTIONS OF BLACK VULTURES (*CORAGYPS ATRATUS*) AND TURKEY VULTURES (*CATHARTES AURA*) IN COSTA RICA AND PANAMA: EVIDENCE FOR RECIPROCAL MIGRATION IN THE NEOTROPICS

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Abstract

We studied the distribution and abundance of Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) in Costa Rica and Panama during northern winter (December-February) and summer (June-July) of 2005. Both species were surveyed along eight routes of 105 to 334 km totaling 1791 km in Costa Rica, and along six routes of 101 to 234 km totaling 963 km in Panama. Black Vultures outnumbered Turkey Vultures in both countries (3:1 in Costa Rica and 5:1 in Panama). Turkey Vulture numbers were similar in winter and summer in Costa Rica (1041 versus 1004), but were substantially higher in winter than in summer in Panama (1413 versus 522). Black Vulture numbers were lower in winter than in summer in Costa Rica (2265 versus 3940), but were higher in winter than in summer in Panama (6352 versus 4245). We did not attempt to determine the subspecies of most of the Turkey Vultures and Black Vultures seen. Nevertheless, our results suggest that migratory North American Turkey Vultures winter in large numbers in central Panama. Given that the winter presence of North American migratory Turkey Vultures is well-documented in Costa Rica; our results also suggest local Turkey Vultures in that country migrate in winter, presumably in response to the arrival of the physically larger North American migrants. Our results also confirm earlier reports by Eisenmann (1963) and Skutch (1969) that Black Vultures also migrate in large numbers in the region. We introduce the term "reciprocal migration" to describe the movements of Neotropical populations of vultures that are made in response to the long-distance migrations of non-tropical North American vultures.

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ABUNDANCIA ESTACIONAL Y DISTRIBUCIÓN DE *CORAGYPS ATRATUS* Y *CATHARTES AURA* EN COSTA RICA Y PANAMÁ: EVIDENCIA DE MIGRACIÓN RECÍPROCA EN LOS NEOTROPICÓS

Resúmen

Estudiamos la distribución y la abundancia de *Coragyps atratus* y *Cathartes aura* en Costa Rica y Panamá durante invierno (diciembre-febrero) y verano (junio-julio) 2005. Ambas especies fueron censadas a lo largo de ocho rutas de entre 105 a 334 kilómetros que suman 1791 kilómetros totales en Costa Rica, y seis rutas de entre 101 a 234 kilómetros que suman 963 kilómetros totales en Panamá. Los *Coragyps atratus* excedieron en número a los *Cathartes aura* en ambos países (2:1 en Costa Rica y 4:1 en Panamá). Los números de *Cathartes aura* en el invierno y el verano en Costa Rica fueron similares (1041 contra 1004), pero fueron considerablemente más altos en el invierno que en el verano en Panamá (1413 contra 522). Los números de *Coragyps atratus* fueron inferiores en el invierno que en el verano en Costa Rica (2265 contra 3940), pero más altos en el invierno que en el verano en Panamá (6352 contra 4245). No intentamos determinar las subespecies de *Cathartes aura* y *Coragyps atratus* vistos. Sin embargo, nuestros resultados sugieren que un gran numero de la población norteamericana migratoria de *Cathartes aura* pasa el invierno en el Este de Panamá. Dado que la presencia durante el invierno de los *Cathartes aura* migratorios de Norteamérica ha sido bien documentada en Costa Rica, nuestros resultados también sugieren que los *Cathartes aura* locales de dicho país emigran en el invierno, en respuesta a la llegada de la población migratoria del norte. También, nuestros resultados confirman las declaraciones de Eisenmann (1963) y Skutch (1969) que los *Coragyps atratu*s también migran en grandes números en la región. Introducimos el término "migración recíproca" para describir los movimientos de las poblaciones neotropicales de buitres (*Coragyps atratus* y *Cathartes aura*) en respuesta a las migraciones de buitres no-tropicales provenientes de Norteamérica.

Introduction

Given the recent and, apparently, continuing catastrophic declines of many populations of Old World Vultures in both southern Asia (Oaks et al. 2003, Green et al. 2004, Cuthbert 2006) and western Africa (Rondeau and Thiollay 2004, Thiollay 2006), Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) now rank as the most common avian scavengers in the world (Ferguson-Lees and Christie 2001). Local and regional abundances of these two species have been little studied outside of Canada and the United States where both species are more abundant in the southeastern and southcentral United States than elsewhere (Kirk and Mossman 1998, Buckley 1999). Black Vultures and Turkey Vultures typically are described as being "common" or "abundant and widespread" in lowlands throughout much of Mexico, south through Costa Rica and Panama (Stiles and Skutch 1989, Ridgely and Gwynne 1989, Howell and Webb 1995), and into Colombia, Venezuela, Ecuador, and Peru (Hilty and Brown 1986, Clements and Shany 2001, Ridgely and Greenfield 2001, Hilty 2003), with Black Vultures being characterized as being particularly obvious near cities and towns.

Studies of migration in these two species have been compromised because of prohibitions on banding in the United States and Canada since the late 1970s, when it was learned that urohidrosis and the subsequent caking of uric acid on bands could hobble individuals (Henckel 1976). Even so, in eastern North America, Turkey Vulture populations of the *septentrionalis* subspecies are believed to migrate largely within the United States and Canada, whereas in western North America, populations of the *meridionalis* subspecies are believed to migrate well into Mexico, Central America, and northern South America (Kirk and Mossman 1998, Bildstein 2006). Season-long, autumn counts at raptor-migration watchsites along the Mesoamerican Corridor in

Mexico, Costa Rica, and Panama, indicate that as many as three million Turkey Vultures migrate through portions of this important flyway (Bildstein and Zalles 2001, Bildstein 2006, E. Ruelas, pers. comm.). Currently, most of these migrants are presumed to belong to the North American *meridionalis* subspecies The extent to which members of the four remaining subspecies of Turkey Vultures, *aura* (southwestern United States, south to about Costa Rica), *ruficollis* (Costa Rica, Panama, and South America east of the Andes), *jota* (western South American highlands from Colombia to Patagonia), and *falklandica* (Pacific lowlands from Ecuador to Tierra del Fuego, Islas Malvinas [Falkland Islands]) migrate is far less well understood, excepting that the population of *falklandica* on the Falkland Islands is, for all intents and purposes, non-migratory (Cawkell and Hamilton 1961, Wetmore 1964). In North America, Black Vultures breeding at the northern limits of the species range are known to evacuate these areas in winter (Buckley 1999). How far they migrate, however, is unknown. Migration in southern Texas-northern Mexico (Donahue 1977a, 1977b; Sexton 1982), Costa Rica (Skutch 1969), and Panama (Eisenmann 1963), while suggested, remains controversial (Jackson 1988, Kirk and Mossman 1998).

In an attempt to assess regional population abundances of the two species and to examine the extent of seasonal changes in populations in northern winter (December-February) versus northern summer (June-July), we surveyed populations of Black Vultures and Turkey Vultures using the roadside-count technique (Fuller and Mosher 1987, Donázar et al. 1993, Sánchez-Zapata et al. 2003). We conducted our counts along primary and secondary roads in Costa Rica and Panama in winter and summer of 2005. Our primary goals were (1) to determine seasonal population abundance and distribution as part of a hemisphere-wide monitoring effort, and (2) to asses the extent of migratory movements in the two species.

Methods

Survey areas, routes, and dates

We surveyed vultures along 1791 km of primary and secondary roads throughout most of Costa Rica, except northeastern Costa Rica northeast of roads connecting the towns of Puerto Viejo de Sarapiqui, Guapiles, Siquirres, and Puerto Limon, because of the lack of appropriate roads there. Our routes on the Pacific slope included more than 90% of the Pan American Highway between the borders with Nicaragua in northwestern Costa Rica and Panama in southern Costa Rica, including the capital of San José. We also surveyed birds along the Pacific coast between Punta Mala and Puntarenas, and on the northeastern portion of the Nicoya Peninsula. Our routes in central Costa Rica included areas within and around the Cordillera Central as far north as the towns of Upala and Los Chiles. Our routes on the Atlantic slope extended from Cartago through Siquirres and Puerto Limon, and southeast to Bribri on the border with Panama (Fig. 1). Eight survey routes were covered in northern winter (31 January through 7 February 2005) and northern summer (3 through 9 July 2005) during the region's dry and wet seasons, respectively. Details of the eight surveys follow:

Costa Rica route 1.--Begins in Cartago southbound on CI 2 (Pan-American Highway) at the Tejar intersection (9°51′41″N, 83°56′48″W); continues on CI 2 to Paso Canoas on the border with Panama (8°32′1.7″N, 82°50′19.9″W). Length, 334 km. Survey dates: 31 January, 4 and 5 July.

Costa Rica route 2.--Begins in Palmar Norte northwest bound on CR 34/18 at intersection with CI 2 (Pan America Highway) (8°57′29.5″N, 83°28′07.6″W); continues northwest on CR 34 to intersection with CR 23 (near Santa Rita), then west on CR 23 to intersection with CR 17 at Roble (9°58′37.9″N, 84°44′23.0″W). Length, 238 km. Survey dates: 1 February, 5 and 6 July.

Costa Rica route 3.--Begins northbound on CR 23 at intersection of CR 17 east of Puntarenas at Roble (9°58′37.9″N, 84°44′23.0″W); continues north to CI 1 (Pan American Highway); then north on CI 1 to the intersection with CR 18 near Limonal; then west on CR 18 via the bridge bypass to intersection with CR 21; then northwest on CR 21 to intersection with CI 1 (Pan American Highway) near Liberia; then northwest on CI 1 to Peñas Blancas on the border with Nicaragua (11°12′21.6″N, 85°36′53.6″W). Length, 273 km. Survey dates: 2 February, 6 and 7 July.

Costa Rica route 4.--Begins southeast-bound on CI 1 (Pan American Highway) at the west end of Liberia (10°37′35.0″N, 85°26′37.6″W) to intersection with CR 6 near Sandillal; then north on CR 6 to the intersection with CR 4 near Upala; then southeast on CR 4 to the intersection with CR 141; then south of CR 141 to the intersection with CR 142 west; then west on CR 142 (CR 735) to San Isidro; then north on CR 142 (CR 735) to Fortuna (10°29′00″N, 84°39′00″W). Length, 226 km. Survey dates: 3 February, 7 July.

Costa Rica route 5.--Begins at Aguas Zarcas at the intersection of CR 250 and CR 140 on CR 140 eastbound (10°22′29.0″N, 84°20′25.2″W); then CR 126 northeast at San Miguel, to intersection with CR 4 east at Bajos de Cilamate; then toward Puerto Viejo de Sarapiqui, to CR 32 east to the "short-cut" road to CR 36 at Pueblo Nuevo via Santa Rosa and Beverly; then on to CR 36 southeast to El Cruce (Hone Creek); then south west of 36 to Bribri (9°37′31.5″N, 82°52′06.0″W). Length, 256 km. Survey dates: 4 February, 8 and 9 July.

Costa Rica route 6.--Begins at Siquirres southwest-bound on CR 10 (10°05′38.7″N, 83°30′39.5″W), to Cartago to intersection with CI 2, then northwest on CI 2 through San José to San Ramon (10°04′N, 84°32′W). Length, 172 km. Survey dates: 5 February, 9 July.

Costa Rica route 7.--Begins at Florencia at the intersection of CR 141 and CR 35 northbound on CR 35 (10°21′39.0″N, 84°28′37.3″W) to border with Nicaragua north of Los Chiles (11°04′30.6″N, 84°41′45.9″W); then backtracks to the intersection of CR 4 and CR 35 (10°27′54.9″N, 84°27′36.8″W), then southeast on CR 4 toward Aguas Zarcas ending at Aguas Zarcas (10°22′29.0″N, 84°20′25.2″W), then on CR 140 east to San Miguel; then restart on CR 126 south (10°18′49.7" N, 84°11′01.8″W) to Hotel Milvia, San Pedro (9°56′N, 84°03′W). Length, 187 km. Survey dates: 6 February, 8 July.

Costa Rica 8.--Begins on CR 39 (San José beltway) southwest-bound (9°55′48.4″N, 84°03′20.2″W); leaves beltway on CR 27 towards Escazú via CR 22 and CR 229 to Santiago (9°51′57.4″N, 84°15′09.5″W), then backtracks to CR 209 toward San Ignacio (9°48′00″N, 84°15′09.5″W); then on 209 to Hotel Milvia in San Pedro (9°56′N, 84°03′W). Length, 105 km. Survey dates: 7 February, 3 July.

We surveyed vultures along 963 km of primary and secondary roads throughout western and central Panama, as far east as Las Aguas Frias in the western Darién, including all of the Pan American Highway (Pacific slope) west to David. We also surveyed vultures between Devisa and Pedasi Cabezas on the eastern side of the Azuero

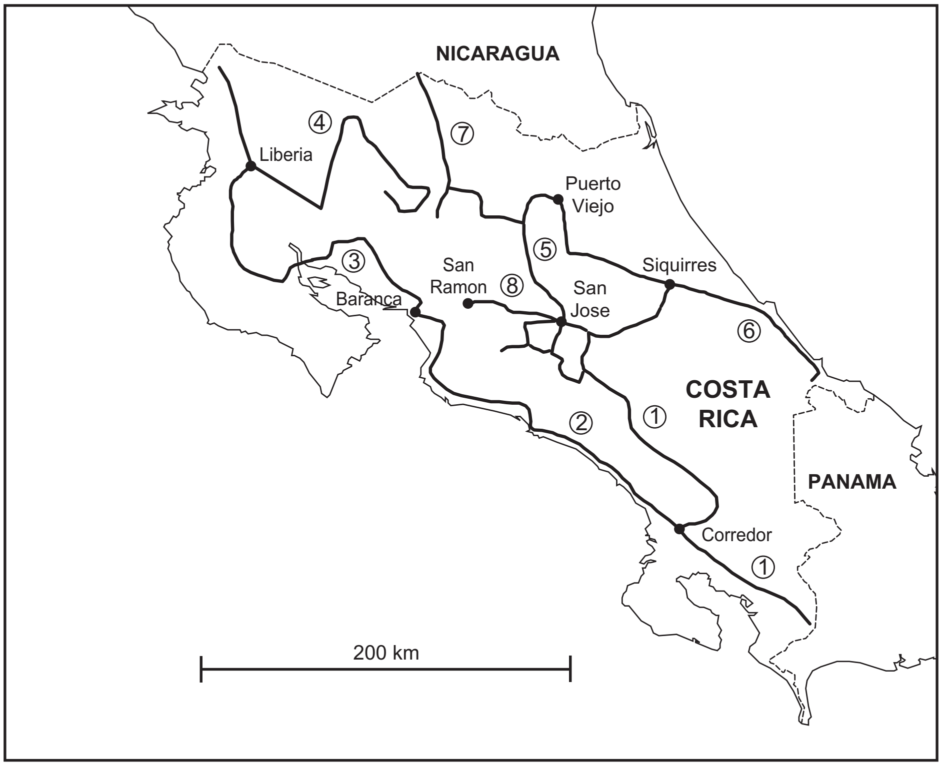

Figure 1. Eight routes along which Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) were surveyed in Costa Rica in northern summer (July) and winter (January and February) 2005. See methods section for details.

Peninsula. In addition to this, two largely north-south routes reached the Atlantic slope, one in western Panama between the town of Chiriqui on the Pacific slope and Laguna de Chiriqui on the Atlantic slope, and the other between Panama City and the colonial city of Portobelo (Fig. 2). Six surveys each were conducted in northern winter (11 through 16 December 2005) and northern summer (27 June through 2 July 2005), at the beginning of the dry and the middle of the wet seasons, respectively. Details of the six surveys follow:

Panama route 1.--Begins Panama City at the McDonald's restaurant at the base of Ancon Hill eastbound on A. Arias Blvd. (8°57′55.9″N, 79°33′12.5″W), to Ave. Balboa; continues on Corredor Sur to Tocumen; then on CA 1 (Pan American Highway) to just beyond Las Aguas Frias at the western end of the Darién (8°48′28.2″N, 78°11′7.8″W). Length, 196 km. Survey dates: 11 December, 27 June 2005.

Panama route 2.--Begins at the western foot of the Bridge of the Americas westbound on CA 1 (Pan American Highway) (8°56′26.0″N, 79°34′21.0″W); continues west on CA 1 to Delta Gas Station approximately 11 km east of Santiago (8°05′03.9″N, 80°52′46.3″W). Length, 234 km. Survey dates: 12 December, 28 June 2005.

Panama route 3.--Begins on CA 1 (Pan American Highway) westbound at the Delta Gas Station east of Santiago (8°05′03.9″N, 80°52′46.3″W); continues west to the main turn-off to David at the Shell Gas Station (8°26′42.5″N, 82°25′20.4″W). Length, 205 km. Survey dates: 13 December, 29 June.

Panama route 4.--Begins at KM-20 marker west of Las Canas on the Bocas Highway (9°01′12.2″N, 82°18′05.9″W) eastbound to the intersection with Lago Fortuna Road near Chiriqui Grande, then on the Lago Fortuna Highway southbound to intersection with CA 1 (Pan American Highway) at Chiriqui (8°23′56.0″N, 82°19′13.5″W). Length, 112 km. Survey dates: 14 December, 30 June.

Panama route 5.--Begins on the Pacific Coast at the southwest corner of the Azuero Peninsula at Playa El Toro near Pedasi (7°31′49.9″N, 80°00′12.1″W) west to downtown Pedasi; then onto PA 2 northwest-bound to the intersection with CA 1 (Pan American Highway) at Divisa (8°07′41.0″N, 80°41′16.5″W). Length, 115 km. Survey dates: 15 December, 1 July.

Panama route 6.--Begins in Albrook at the Rey Supermercado (8°58′20.5″N, 79°33′52.6″W) northbound along the Panama Canal on Roosevelt Blvd. to the intersection with PA 3 (the Boyd-Roosevelt Highway); then northwest-bound to turnoff to Portobelo at the Rey Supermercado at Sabanita; then to the Agriculture Building approximately one km east of the center of Portobelo (9°33′11.6″N, 79°38′23.3″W). Length, 101 km. Survey dates: 16 December, 2 July.

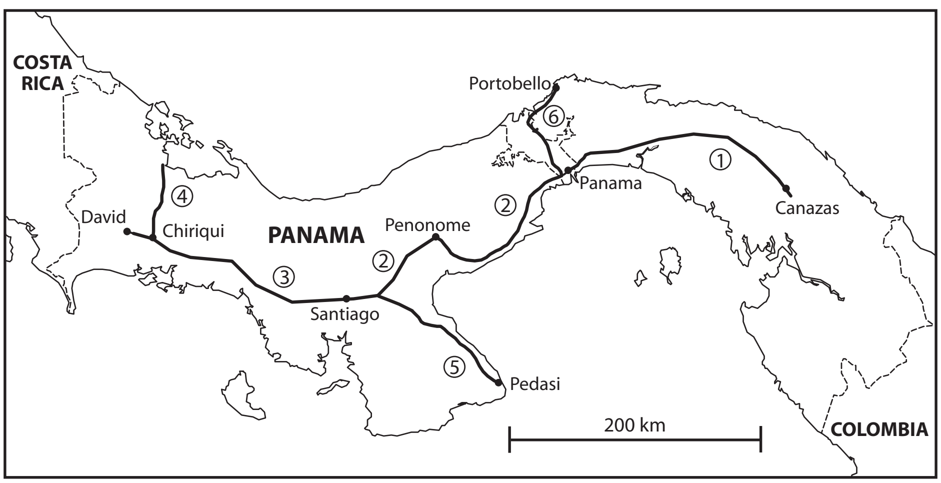

Figure 2. Six routes along which Black Vultures (*Coragyps atratus*) and Turkey Vultures (*Cathartes aura*) were surveyed in Panama Rica in northern summer (June and July) and winter (December) 2005. See methods section for details.

Survey protocols

Our counts were completed using methods employed in similar geographically extensive roadside surveys (e.g., Donázar et al. 1993, Sánchez-Zapata et al. 2003). Specifically, we (1) limited our counts to times of the year when vultures were not migrating in the survey area, and to times of the day (i.e., 0930 through 1530), when vultures were likely to be foraging rather than ferrying themselves to and from nocturnal roosts (Kirk and Currall 1994), (2) surveyed 100 to 300 km each day, (3) recorded the latitude and longitude at the start and end of each survey, as well as the road number(s) and any beginning and ending and intersectional place names, (4) traveled at speeds of 30-60 km per hour (i.e., 19-37 mph), (5) used a driver and one or two observers whenever possible, (6) recorded percent cloud cover, wind, and temperature at the beginning and end of each survey, (7) limited our counts to rainless periods, or periods interrupted by rains of fewer than 5 minutes, (8) recorded the locations of all vultures seen to the nearest tenth of a kilometer, (9) recorded all birds seen, including both perched and flying individuals, and (10) stopped when needed to identify distant birds to genus, as well as to count the numbers of individuals in large flocks, but when stopped, included only those birds initially spotted and not any new birds sighted after stopping. Three subspecies of Turkey Vultures (*meridionalis* [winter only], *aura* [Panama winter only], and *ruficollis* [presumably Panama only]), and Lesser Yellow-headed Vulture (*C. burrovianus*) occur in our survey areas (Wetmore 1964, Ridgely and Gwynne 1989, Stiles and Skutch 1989). Separating these four *Cathartes* in the field can be difficult at times, particularly when traveling along roads at 30 to 60 km per hour. Although we did not attempt to characterize all of the *Cathartes* vultures we counted to species or subspecies, the overwhelming majority of those that we did characterize belonged to one of the three subspecies of Turkey Vultures and were not Yellow-headed Vultures. Thus, for the purposes of our analysis we considered all *Cathartes* counted to have been Turkey Vultures.

Statistical analyses

For the purpose of comparative analyses, we divided our count routes into three regions: Costa Rica, western Panama, and central Panama. Costa Rica included all eight Costa Rican count routes; western Panama included Panama count routes 3, 4, and 5 (i.e., the area west of Santiago, including all of the Azuero Peninsula); and central Panama included Panama count routes, 1, 2, and 6 (i.e., Santiago east to the westernmost Darién) (Figs. 1 and 2). We then divided all of our survey routes into 50-km sections, and used two-tailed, paired *t*-tests to test for seasonal and species differences in numbers. We used SAS version 9.1 software (SAS Institute, Inc. 2002) to analyze our data, and considered statistical significance to be $P \leq 0.05$.

Results

During the winter and summer of 2005 we counted totals of 2265 and 3940 Black Vultures and 1041 and 1004 Turkey Vultures in Costa Rica, and 6352 and 4245 Black Vultures and 1413 and 522 Turkey Vultures in Panama, respectively. Black Vultures outnumbered Turkey Vultures in both countries, both in winter and in summer (2.1:1 and 3.9:1 in Costa Rica [$t_9 = -3.76$, $P = 0.002$; $t_8 = -4.21$, $P = 0.001$], 4.5:1 and 7.5:1 in Panama [$t_5 = -3.54$, $P = 0.008$; $t_5 = -3.51$, $P = 0.009$]). Turkey Vulture numbers were similar in winter and summer in both Costa Rica ($t_{28} = -0.07$, $P = 0.94$) and in western Panama ($t_7 = -0.53$, $P = 0.6$), but were significantly higher in winter than in summer in central Panama ($t_9 = 3.81$, $P = 0.004$) (Table 1). Black Vulture numbers were significantly lower in winter than in summer in Costa Rica ($t_{28} = -2.92$, $P = 0.007$), similar in winter and in summer in western Panama ($t_7 = 0.02$, $P = 0.98$), and markedly (i.e., 132%), although not significantly so, higher in winter than in summer in central Panama ([$t_9 = 1.94$, $P = 0.08$) (Table1).

Table 1. Numbers of Black Vultures and Turkey Vultures (± standard error of the mean) seen on 50-km sections of roadside counts in Costa Rica, western Panama, and central Panama in northern winter (December-February) and summer (June-July) 2005.

		Vultures per 100 km (± SE)		
Species	Season	Costa Rica	Western Panama	Central Panama
Black Vulture	Winter	154.3 (21.8)	628.3 (266.9)	740.4 (213.3)
	Summer	228.6 (27.2)	624.8 (285.6)	318.6 (22.5)
Turkey Vulture	Winter	63.6 (6.6)	85.3 (17.3)	211.6 (42.9)
	Summer	64.1 (1.5)	92.5 (10.4)	33.4 (4.9)

Discussion

We are unaware of any earlier roadside counts of Black Vultures in Costa Rica or Panama. There is one earlier roadside count of Turkey Vultures in the region. In December of 1977 Neal Smith (1980) "surveyed Turkey Vultures along the Pan American Highway from the Costa Rican border to Panama City," the same road we counted Turkey Vultures along on 12 and 13 December 2005. Unfortunately, Smith did not describe his survey techniques in detail. From information presented in his paper we believe that he conducted his survey alone and that he stopped at least infrequently en route to identify Turkey Vultures to subspecies (Smith 1980). Smith reported 849 Turkey Vultures per 100 km, whereas we counted 146 per 100 km. We suggest three, non-exclusive possibilities for the almost six-fold difference in densities reported during these two winter surveys. The first is that winter populations of Turkey Vulture in western Panama collapsed catastrophically between 1977 and 2005. We believe that this is not probable for several reasons. First, given the numbers of birdwatchers and ornithologists that regularly visit Panama, it seems unlikely that a collapse of this magnitude would have gone unnoticed along this major thoroughfare. Second, there is no indication of a long-term decline in the numbers of Turkey Vultures seen on Christmas Bird counts in Panama between 1991 and 2004 (http://www.audubon.org/bird/cbc/hr/index). Third, wintertime surveys of two species of *Cathartes*, Turkey Vultures and Lesser Yellow-headed Vultures, in coastal northern Colombia in 1978-1980 conducted by two observers using techniques similar to ours, including not counting vultures while stopped, reported counts of 280 birds per 100 km for both species combined, or about one third of Smith's counts of Turkey Vultures alone. Even so, it is possible that the numbers of Turkey Vultures wintering in the region have declined somewhat since the late 1970s, and we urge that additional counts in this part of the country be undertaken soon to determine the stability of current wintering populations there.

A second possible explanation for at least part of the difference between Smith's results and ours is methodological. Smith most likely stopped frequently during roadside counts as his principal purpose in conducting the surveys was to determine the ratio of migrant to resident Turkey Vultures in the region, and the subspecies involved often are difficult to separate while surveying from a moving vehicle (Koester 1982). Stopping en route substantially increases the numbers of vultures counted on roadside surveys (Ellis et al. 1983, K. L. Bildstein, pers. obs.). If Smith did stop frequently and counted vultures after doing so, he is likely to have increased his counts considerably.

A third possible explanation for the difference is that Smith may have conducted his survey when large numbers of migrants where still passing through the region. A later than usual vulture migration in 1977 that resulted in the presence of even a relatively small percentage of the more than one-million-bird flight of migrating Turkey Vultures that passes through the region into early December (Bildstein and Zalles 2001, Porras-Peñaranda et al. 2004), easily could have increased vulture numbers several fold.

Black Vultures outnumbered Turkey Vultures along our survey routes in all three regions. We know of three other roadside surveys that simultaneously surveyed these two species in the Neotropics. The first, a continent-wide count that surveyed areas from northern South America through southern South America recorded both species along 10 of 23, 79- to144-km surveys in seven countries in South America (Ellis et al. 1990). Black Vultures clearly outnumbered Turkey Vultures in three of the surveys, one each in northcentral Venezuela (winter), southcentral Brazil (winter), and northeastern Argentina (spring); and Turkey Vultures clearly outnumbered Black Vultures in one winter survey in northeastern Venezuela (Ellis et al. 1990). Unfortunately, results from the other six surveys do not clearly indicate the relative abundances of the two species. A second survey (Donázar et al. 1993) that counted individuals along 1234 km of roads in the northern Argentinean Patagonia, a region in which neither species is particularly abundant (Ferguson-Lees and Christie 2001), found Turkey Vultures to be more numerous than Black Vultures. A third survey (Reichholf 1974) that counted raptors, including Black Vultures and Turkey Vultures, in southern Brazil, Paraguay, and eastern Bolivia, found that Black Vultures greatly outnumbered both Turkey Vultures overall.

In addition to these roadside counts, Kirk and Currall (1994) used point counts to simultaneously survey populations of Black Vultures and Turkey Vultures throughout the year in the Llanos of northcentral Venezuela in 1984-1987. They reported that Turkey Vultures outnumbered Black Vultures in winter, but that Black Vultures outnumbered Turkey Vultures at other times of the year, a phenomenon they convincingly tied to the arrival and departure of northern migratory Turkey Vultures (Kirk and Currall 1994, Kirk and Gosler 1994). Taken as a whole, these studies, together with ours, suggest that in the equatorial Neotropics, Black Vultures outnumber Turkey Vultures, at least in summer. That said, considerable geographic variation exists in the relative abundances of these two species in the Neotropics and much remains to be learned regarding their relative numbers there.

Our surveys indicate substantial seasonal shifts in the numbers of both Black Vultures and Turkey Vultures in all three regions surveyed. In winter, numbers of Black Vultures declined by 33% in Costa Rica, remained the same in western Panama, and increased by 132% in central Panama (Table 1). By comparison, in winter, numbers of Turkey Vultures remained the same in both Costa Rica and western Panama, but increased by more than 500% in central Panama (Table 1). We believe that for both species the differences result from migratory movements.

Turkey Vultures

The more than five-fold wintertime increase in Turkey Vulture numbers falls within the range of the seven-fold and four- to five-fold wintertime increases for this species reported by Koester (1982) for Caribbean lowland Colombia and by Kirk and Currall (1994) for central Venezuela, respectively. Both of these studies convincingly attributed these seasonal differences to the arrival of large numbers of migrants from North America. Full-season autumn counts of Turkey Vultures migrating across the

Panama Canal in central Panama in autumn 2004 and 2005 indicate that more than one-million "northern" Turkey Vultures regularly reach central Panama. Furthermore, the sighting of a wing-tagged migrant from Saskatchewan, Canada, at the Maracaibo Zoo in northwestern Venezuela in the winter of 2005 (S. Houston, pers. comm.) demonstrates that at least some of these birds reach Venezuela. We believe that the more than five-fold increase in Turkey Vultures numbers we recorded in central Panama in winter reflects the arrival of these birds in that region.

The lack of similar increases in Turkey Vulture numbers in Costa Rica and western Panama is more difficult to explain. Stiles and Skutch (1989) report overwintering migrant Turkey Vultures "principally in the lowlands" for Costa Rica, and Smith (1980) reported that 45% of Turkey Vultures he observed in Panama west of the Panama Canal in December of 1977 were migrants. Assuming this to be true, then the lack of increased numbers of Turkey Vultures in the winter of 2005 in Costa Rica and western Panama either reflects a substantial shift in the migration destinations of northern migrants since these earlier accounts or, perhaps more likely, that some of the birds generally assumed to be *meridionalis* migrants from Canada and the United States, are, in fact, members of the *aura* subspecies, which breeds from the southwestern United States into central Costa Rica and, possibly, the *ruficollis* subspecies, which breeds from Costa Rica through Panama and into northern South America (Wetmore 1964). *Aura* movements in particular seem likely as Wetmore (1964) stated that this subspecies wintered "south through Panama to Darien," suggesting that it migrated in the region. Although "chain migration" (i.e., migration in which migratory populations that breed at high latitudes migrate approximately the same distance as those that breed at lower latitudes) is less frequently reported in raptors than is "leapfrog" migration (i.e., migration in which migratory populations that breed at high latitudes migrate substantially farther than and "leap over" migratory and non-migratory populations breeding at lower latitudes) (Bildstein 2006), the results of our counts lead us to conclude that both chain and leapfrog migration may occur in Turkey Vultures in the region and that migrants in the region include members of all three subspecies, with northern *meridionalis* replacing some but not all *aura* and *ruficollis* in the region.

Black Vultures

Eugene Eisenmann (1963), and Alexander Skutch (1969) were the first to propose that Black Vultures migrated in Panama and Costa Rica, respectively. Eisenmann reported that while engaged in other work he "observed during many days in November 1962, groups of up to about 100 "Black Vultures moving eastward, seemingly toward South America," the same direction he had earlier seen Turkey vultures migrating in, and often in the company of migrating hawks (Eisenmann 1963). Skutch noted that when looking for them along a ridge outside of San José in 1964 "Black Vultures passed southward, on almost every morning that [he] looked for them from 8 September (if not earlier) until [my] departure in early December," and that the birds he observed were traveling in loose flocks of 25 to 50 individuals (Skutch 1969). He also mentioned having observed springtime, northwest flights of Black Vultures that resembled those of migratory Broad-winged Hawks (*Buteo platypterus*) (Skutch 1969). Although neither of these observers was able to determine the origins or destinations of the birds they observed, Eisenmann suggested that the birds he watched were juveniles that were migrating and that breeding adults were more sedentary (Eisenmann 1963). Our observations of co-incidental decreases in numbers in Costa Rica and increases in numbers in central Panama suggest that at least some of the Black Vultures Skutch and Eisenmann watched may have been moving within the region, rather than through it. On the other hand, the increased numbers of Black Vultures we recorded in central Panama may have been moving to locations farther east. Whatever the destinations and origins of the birds involved, our observations support the notion of Black Vulture migration in the region.

Why local populations of Black Vultures and Turkey Vultures migrate within the tropics is not immediately apparent. Declines in food resources in winter are not obvious, and in late autumn *meridionalis* Turkey Vultures are moving into some of the same areas that local Black Vultures and local Turkey Vultures are moving out of. We believe the intra-tropical movements of Black Vultures and Turkey Vultures, presently, are best explained by intra- and inter-species competition for food within the region's avian scavenger guild. Northern Turkey Vultures are larger overall than their tropical counterparts (Wetmore 1964, Kirk and Gosler 1994), and the former are known to behaviorally dominate the latter at carcasses (Koester 1982, Kirk and Gosler 1994, Kirk and Houston 1995). Moreover, although Turkey Vultures in North America are believed to be subordinate to the *atratus* subspecies of Black Vultures they encounter there (Stewart 1978), the Black Vultures that northern Turkey Vultures interact with in the tropics belong to the smaller *brasiliensis* race (Wetmore 1964), and Koester (1982) reports that the northern Turkey Vultures are capable of holding their own against tropical Black Vultures at dumps in and around cities in northern Colombia. Whether this competitive advantage is due to the relative sizes of the birds involved, to the fact that migrant Turkey Vultures tend to feed in larger groups than resident Turkey Vultures (Kirk and Houston 1995), or to some other reason, we suggest that migrant Turkey Vultures dominate local vultures to the extent that the latter redistribute themselves to avoid the former. Some tropical individuals do so by dispersing short distances into suboptimal habitats unoccupied by the migrants (Koester 1982, Kirk and Currall 1994). Our results indicate that others migrate longer distances in response to the arrival of northern migrants. We refer to this type of migration as "reciprocal migration," because it occurs in response to the arrival of other migrants and a subsequent reduction in available resources for local birds.

If tropical populations of vultures are forced to move short and long distances and, in some cases, inhabit sub-optimal habitats in response to the arrival of large numbers of Turkey Vultures from North America, then tropical populations, and, indeed, entire tropical communities of vultures may be restricted by the seasonal occurrence of these migratory populations. The extent to which interactions between temperate-zone and tropical vultures affect the breeding seasonality, success, and overall abundance of tropical vultures remains a largely unexplored topic (but see Kirk and Houston 1995) that deserves additional study.

Finally, our surveys convince us that much remains to be learned about the geography of vulture migration in the Neotropics. We strongly recommend that studies of what appears to be a relatively complex pattern of movements be undertaken as soon as possible.

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