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WINTER RANGES OF MIGRATORY TURKEY VULTURES IN VENEZUELA

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Abstract.—We used four Global Positioning System (GPS) satellite transmitters to calculate the wintering ranges of migratory Turkey Vultures (*Cathartes aura*) that breed in Saskatchewan, Canada, and winter in Venezuela. Between 2007 and 2011, 95% fixed-kernel estimators of range size varied from 54 to 76 731 km² with an average of 16 814 ± 28 606 km² (SD), while those calculated with 95% Minimum Convex Polygons ranged from 22 to 46 778 km² and averaged 9545 ± 17 356 km². The smallest wintering range was comparable to previously reported range sizes, but our largest wintering range greatly exceeded anything yet recorded. Variation in winter range sizes may be attributed to resource availability, migration costs, and the absence of obligations associated with breeding. Each vulture had a ''primary nocturnal roost'' to which it returned frequently; each spent more hours (evenings, nights, and mornings) at and within 1 km of such roosts, than it did foraging during midday. Our results increased our understanding of the feeding and movement ecology of North American migratory Turkey Vultures overwintering in South America.

Key Words: *Turkey Vulture*; Cathartes aura; *migration*; *winter range*; *Venezuela.*

ÁREAS DE INVERNADA DE INDIVIDUOS MIGRANTES DE *CATHARTES AURA* EN VENEZUELA

Resumen.—Utilizamos cuatro transmisores satelitales de Sistema de Posicionamiento Global (SPG) para calcular las áreas de invernada de individuos de *Cathartes aura* que se reproducen en Saskatchewan, Canadá e invernan en Venezuela. Entre 2007 y 2011, 95% de los estimadores de kernel fijo del tamaño de área variaron de 54 a 76 731 km² con un promedio de 16 814 ± 28 606 km² (DE), mientras que aquellos calculados con 95% de los Polígonos Convexos Mínimos variaron de 22 a 46 778 km² y promediaron 9545 ± 17 356 km². El área de invernada más pequeña fue comparable con los tamaños de área reportados previamente, pero nuestras áreas de invernada más grandes excedieron por mucho a cualquiera registrada hasta ahora. La variación en los tamaños de las áreas de invernada puede ser atribuida a la disponibilidad de recursos, los costos migratorios y la ausencia de obligaciones asociadas con la reproducción. Cada buitre tuvo una ''percha nocturna principal'' a la que retornaba frecuentemente; cada

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uno permaneció más horas (tardes, noches y mañanas) en dicha percha y a 1 km alrededor de ella, que las que dedicó a alimentarse durante el mediodía. Los resultados aumentaron nuestro entendimiento sobre la ecología de forrajeo y de movimiento de individuos norteamericanos migratorios de *C. aura* invernando en América del Sur.

[Traducción del equipo editorial]

Ranging from Canada to the southern tip of South America, the Turkey Vulture (*Cathartes aura*) is arguably the most abundant and widespread vulture in the world (Ferguson-Lees and Christie 2001). It is also the most migratory of all avian scavengers (Mundy et al. 1992, Bildstein 2006). Many Turkey Vultures in North America, especially those breeding at higher latitudes, migrate to wintering grounds in the southern United States, Mexico, Central America, and northern South America (Chapman 1933, Kirk and Mossman 1998, Mandel et al. 2011). Recently, satellite tracking has revealed that Turkey Vultures breeding in La Pampa, Argentina, migrate north into Bolivia and Brazil during the austral winter (K. Bildstein unpubl. data). We also believe that Central American and northern South American Turkey Vultures exhibit reciprocal migration after being ousted from preferred areas by their dominant North American counterparts (Bildstein et al. 2007). Little is known, however, of the movements of North American Turkey Vultures after they arrive on their Central and South American wintering areas.

Turkey Vultures are opportunistic scavengers that feed primarily, if not entirely, on carrion (Kirk and Mossman 1998), and that adjust their daily movements based on where and when food becomes available (Coleman and Fraser 1989, McLoughlin and Ferguson 2000, Houston et al. 2011). Carrion can be unpredictable locally, and broad variation in previously reported home ranges both within and among geographic areas most likely reflects this. To date, nonbreeding summer home-range sizes have been described for individuals that overwinter in the central and southern United States (Coleman and Fraser 1989 [69 km^2, n = 1]; Arrington 2003 [10 km^2, n = 1]). Breeding home ranges (n = 6) of the Saskatchewan birds have been described by Houston et al. (2011). There are, however, few data describing the movements and ranges for Turkey Vultures that migrate south of the United States. Our goal was to help fill this gap by documenting the sizes of home ranges of vultures wintering in Venezuela.

METHODS

Study Area. We tracked the daily movements of four vultures that wintered in the Llanos wetlands of Venezuela, after migrating from Saskatchewan, Canada (cf. Houston et al. 2011). Spanning an area of 275 000 km^2, the Llanos is bounded by mountains, the Cordilera de Merida in the north and the Andes in the northwest, the Orinoco River Delta in the southeast, and the Colombian border in the south (Mittermeier et al. 2003). The Llanos covers approximately 31% of Venezuela and is characterized by its complex mosaic of habitats consisting of wetlands with scattered palms, moist gallery forest, dry tropical forest, and generally poor soil conditions contributing to an often minimal fragmented presence of agriculture (Jensen et al. 2005, Vilella and Baldassarre 2010). Rainfall is highly seasonal in the area, with most rain occurring between May and September, when significant flooding occurs (Vilella and Baldassarre 2010). The dry season spans from November to March, and although open-water areas are reduced during this time, the composition of savanna vegetation remains similar (Hamilton et al. 2002).

Breeding Location and Satellite Transmitters. We captured four adult Turkey Vultures on their eggs or small young in central Saskatchewan, Canada, and equipped each with an alphanumeric patagial tag on the left wing and a 40-g backpack-style solar-powered Global Positioning System (GPS) satellite transmitter. Two of these units (65544 and 65545 [Microwave Telemetry, Columbia, Maryland, U.S.A.]) were attached 16 and 17 June 2007, with patagial tags H8 and T2, respectively. The satellite transmitters provided locations on an hourly basis (for approximately 85% of possible hr while deployed). On 22 May 2009, two other birds were given patagial tags T3 and T4 and transmitters 85753 and 85754 (North Star Science and Technology, King George, Virginia, U.S.A.), which provided locations every 3 hr. All transmitters were $<$4% of the body mass of the birds to which they were attached. All four transmitters had an accuracy of $\pm$10 to 15 m. Vultures T3 (male) and T4 (female) were captured at the same nest site and were selected for sex determination from DNA

Table 1. Movements of four adult Turkey Vultures equipped with transmitters in Saskatchewan, Canada, upon arrival and departure on their wintering grounds in Venezuela. Arrival and departure locations were nearly identical in seven of nine instances.

Patagial Tag	Transmitter	Year Tagged	Arrival at First Nocturnal Roost					Departure from Final Nocturnal Roost					Km Between First and Last Roost
			Date	Year	Time AST	Lat	Long	Date	Year	Time AST	Lat	Long	
H8	65544	2007	18 Jan	2008	1600	8.09017	68.792	18 Mar	2008	0700	8.0915	68.59967	21
T2 first year	65545	2007	18 Nov	2007	2000	7.30817[a]	69.86867	18 Mar	2008	0700	7.30767[a]	69.869	2
T2 second year	65545		18 Nov	2008	2000	7.30767[a]	69.88687	19 Mar	2009	0800	7.30767[a]	69.86883	0
T2 third year	65545		21 Nov	2009	1700	7.30783[a]	69.869	20 Mar	2010	0700	7.30717[a]	69.86983	0
T2 fourth year	65545		1 Nov	2010	1700	7.30967	69.85483	21 Mar	2011	0600	7.30767[a]	69.86883	2
T3 first year	85753	2009	12 Nov	2009	2000	8.8756	69.1452	24 Mar	2010	1100	9.5188	69.0036	73
T3 second year	85753		31 Oct	2010	2000	9.7736	70.2546	15 Mar	2011	0800	8.5332	70.1294	139
T4 first year	85754	2009	16 Dec	2009	2000	9.7325	63.7283	26 Mar	2010	0800	9.7704	63.6833	6
T4 second year	85754		20 Nov	2010	2000	9.7806[a]	63.6856	29 Mar	2011	0800	9.7812[a]	63.685	0

[a] Primary nocturnal roost of bird.

extracted from feathers (Health Gene Laboratories, Toronto, Ontario, Canada). The sex (female) of T2 was determined by observing copulation in 2011 (M. Stoffel unpubl. data). The sex of vulture H8 was not determined. Three vultures were tracked in consecutive winters but H8 died 2 December 2008 in Limon, Costa Rica, while on its second southward migration.

Wintering Home Ranges. We determined the specific wintering area of each vulture from its arrival at the end of its continuous migration route until its departure on its continuous migration return to Saskatchewan. In seven of nine instances, the arrival location and departure location were almost identical (Table 1); the resulting dates bounded each home-range estimation. The unusually consistent migration pathways connecting the breeding and nonbreeding locations for the years 2006 and 2007 were mapped in Fig. 2 of Mandel et al. (2011).

We used the methods of Houston et al. (2011) to determine wintering range size (Table 2). Using the Home Range Estimator extension for ArcView 3.2, we applied both 95% minimum convex polygons (MCP) and 95% fixed-kernel home-range estimators to the vulture's locations. Outputs from the fixed-kernel method are assumed to be more accurate because the calculated ranges minimize the inclusion of outlying locations (Kernohan et al. 2001, Hasselblad and Bechard 2007, Houston et al. 2011); however, we also included MCP ranges as a standard for comparison. To reduce temporal autocorrelation, we resampled our large data sets, which were composed of multiple points per day, to one randomly chosen point per day (Schoener 1981, Swihart and Slade 1985, following Houston et al. (2011)). Statistical analysis was performed in Minitab v. 16 (Brook 2010). We present data as means ±1 SD.

Characteristics of Winter Roost Sites. On 8 May 2012, MJB visited the wintering roost that female T2 occupied in four consecutive winters, 2007–2011. MJB used a handheld GPS unit to drive to the primary nocturnal roost site of T2 at 7.30°N and 69.86°W, in the southwestern Llanos, and interviewed the farm owner at the roost about vultures using the area, and measured the height of roost trees with a clinometer, and the diameter at breast height (DBH) with a tape.

RESULTS

The earliest and latest vultures to arrive on their wintering grounds did so on 31 October 2010 (T3)

Table 2. Annual nonbreeding wintering ranges for four Turkey Vultures in Venezuela from 2007–11. 95% fixed kernel and 95% MCP ranges were calculated from a subsample composed of one randomly chosen location per day for each nonbreeding season. Vulture ID indicates the patagial tag assigned to each bird.

VULTURE ID	TRANSMITTER	YEAR	START DATE	END DATE	SEX	n	95% KERNELS (km²)	95% MCP (km²)
H8	65544	2008	18 Jan 2008	17 Mar 2008	Unk	46	167	93
T2	65545	2007–2008	17 Nov 2007	18 Mar 2008	F	123	14 243	4606
T2	65545	2008–2009	11 Nov 2008	19 Mar 2009	F	129	1895	1286
T2	65545	2009–2010	21 Nov 2009	20 Mar 2010	F	117	1915	1071
T2	65545	2010–2011	2 Nov 2010	22 Mar 2011	F	141	1046	469
T3	85753	2009–2010	14 Nov 2009	24 Mar 2010	M	130	54 698	32 166
T3	85753	2010–2011	3 Nov 2010	14 Mar 2011	M	131	76 731	46 778
T4	85754	2009–2010	17 Dec 2009	26 Mar 2010	F	100	581	314
T4	85754	2010–2011	20 Nov 2010	29 Mar 2011	F	128	54	23
Mean ± SD						116 ± 29	16 814 ± 28 606	9645 ± 17 356

and 18 January 2008 (H8), respectively. The earliest and latest departures occurred on 15 March 2011 (T3) and 29 March 2011 (T4), respectively. The wintering season spanned an average of 117 ± 25 d (Table 1). Because the vultures from Saskatchewan are in Venezuela during the Llanos dry season when precipitation and cloud cover are low, our transmitters received strong satellite signals and we were able to log an average of 20 points per day for H8 and T2, and 7 points per day for T3 and T4 in all years. Thus, each transmitter supplied between 697 and 2727 locations with an average of 1713 ± 921 (SD) points during the season. We resampled the data set for analyses to one point per day which averaged 116 ± 29 points per bird per winter year (Table 2). Wintering ranges obtained from the 95% MCP method averaged 9545 ± 17 356 km², whereas those obtained from the fixed-kernel method averaged 16 814 ± 28 606 km² (Table 2, Fig. 1). The largest range was 76 731 km² with 95% fixed kernels, and 46 778 with 95% MCP. The smallest was 54 km² with 95% fixed kernels and 22 km² with 95% MCP (Table 2, Fig. 1, 2). The two methods differed at only $\alpha = 0.10$ (paired two-sample t-test $t = 1.89$ and $P = 0.096$), though we acknowledge that power was low.

Each vulture used a ''primary nocturnal roost'' to which it returned frequently (e.g., T2, Fig. 3). Each spent an average of 15 hr (evenings, nights, and mornings) at and within 1 km of such roosts. Mean arrival at the nocturnal roost varied among years from 17:19 to 18:25 H Atlantic Standard Time. Female vulture T2 (Fig. 3) wintered in western Venezuela and spent 316 of 497 nights over four successive years at her primary nocturnal roost. The roost, adjacent to a farm house, was in a 6-ha grove of mature water palms (*Attalea butyracea*) with an average DBH of 43.5 ± 2.8 cm ($n = 10$) and average height of 18.2 ± 4.6 m ($n = 10$). The farm owner reported that palms in the area had been planted more than 100 yr ago. The understory was mixed banana (*Musa acuminata*), mango (*Mangifera indica*), and various fruit trees. Twenty to 100 Turkey and Black (*Coragyps atratus*) vultures used the roost year-round, with the numbers increasing from November to March. The surrounding savanna was pasture for cattle and horses, with native mammals such as capybara (*Hydrochaeris hydrochaeris*) and flocks of waterfowl and wading birds (M. Bechard unpubl. data).

Because our winter ranges were calculated for the same individuals on their breeding grounds in Saskatchewan (Houston et al. 2011), we could make direct comparisons between breeding and wintering range sizes for the same individual vultures (Table 3).

Vulture H8 in 2007 had an unusually slow southward migration with its southbound trip of 6014 km from Saskatchewan to Venezuela averaging only 53 km/d. While on its winter territory, it also was unique in that it never moved more than 100 km/d nor reached 500 m aboveground.

DISCUSSION

We found much greater variation in the winter ranges of Turkey Vultures than in breeding ranges in North America. (Houston et al. 2011). The largest winter range in Venezuela exceeded the largest breeding range in North America by 95%, or by

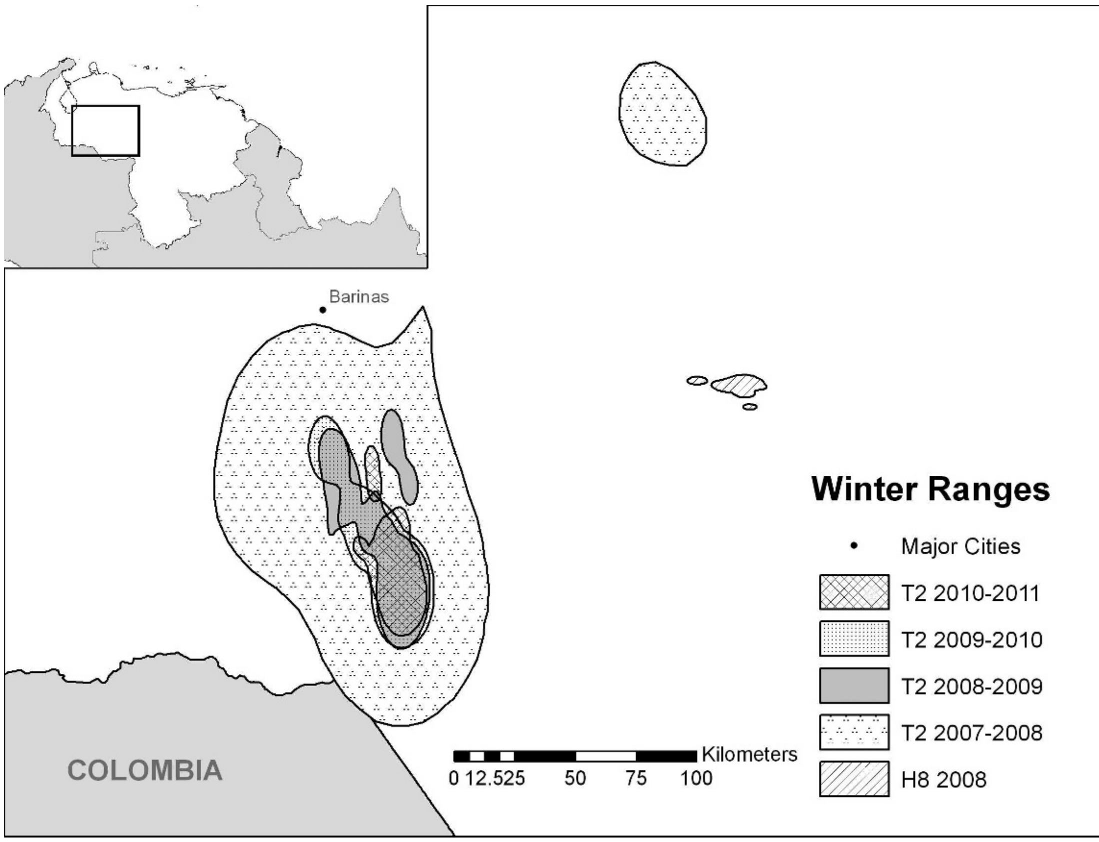

Figure 1. Locations of winter ranges in Venezuela (95% fixed-kernel) of Turkey Vultures H8 (transmitter 65544, 2007), and T2 female (transmitter 65545, 2007–11).

74 739 km^2, whereas the smallest winter range in Venezuela was comparable to breeding ranges in North America (Coleman and Fraser 1989, Arrington 2003, Houston et al. 2011). Although many factors influence home-range size in birds (Peery 2000), food availability is considered to be the primary determinant (Rolando 2002). The Llanos of Venezuela is a complex mosaic of habitats that contribute to differing levels of biological productivity (Mittermeier et al. 2003), which may account for the variation in winter ranges that we observed.

Recently published records of year-round ranges of Turkey Vultures in South Carolina varied from 91 to 482 km^2 (n = 3 adult vultures, sex unknown, none of which was a proven breeder; DeVault et al. 2004, T. DeVault, pers. comm.). In comparison, the winter ranges of the Saskatchewan-breeding pair T4 (female) and T3 (male) were separated by 223 km at their closest point. They differed greatly in size (Fig. 2), with the male displaying the largest wintering range (76 731 km^2 in 2010–11), whereas the female had the smallest (54 km^2 in 2010–11). In Saskatchewan they had shared virtually the same small breeding range (Houston et al. 2011). Why there should be this difference between sexes during winter, and the lack of similar contrasts for vultures wintering in southern North America, is unknown.

Turkey Vulture flight almost exclusively involves thermal soaring (Bohrer et al. 2012). Turkey Vultures largely forego feeding during their long-distance migrations (Bildstein 2006), and on average require 40 d to regain lost body mass after they arrive in Venezuela (Kirk and Gosler 1994). The difference between wintering ranges in Venezuela and those in South Carolina may be explained largely by carrion availability; both areas benefit from communal foraging in winter.

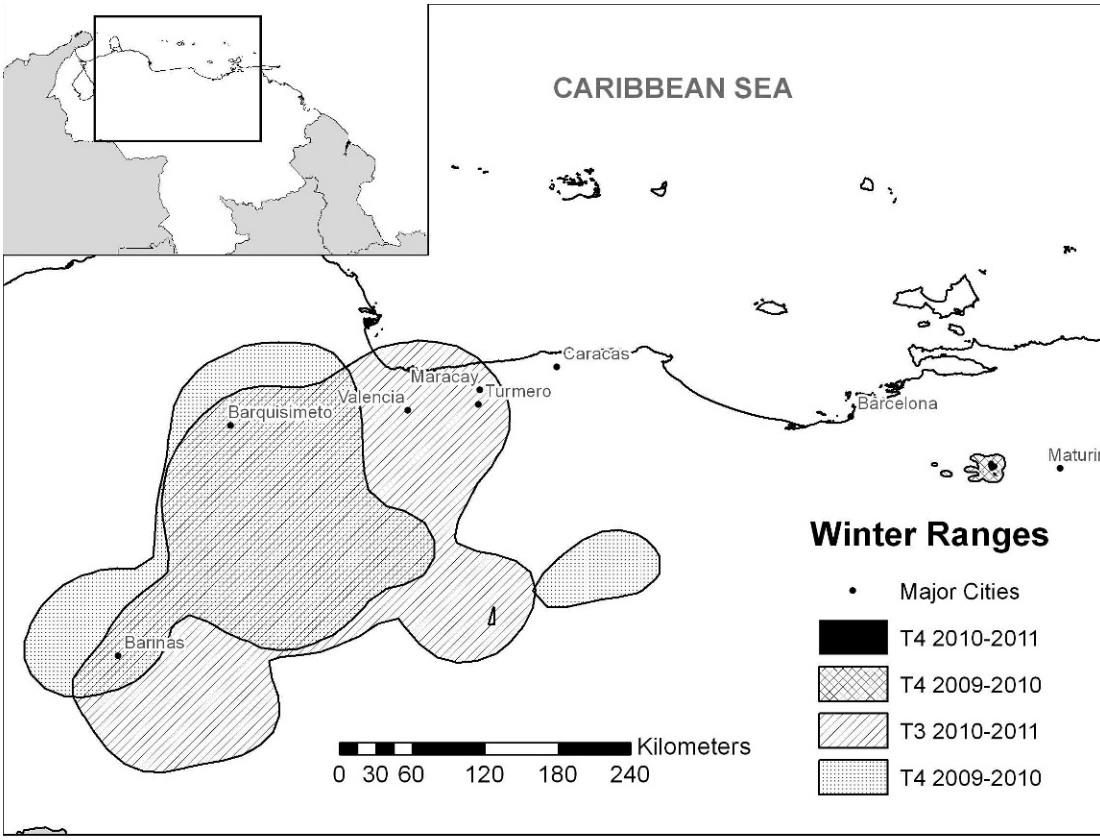

Figure 2. Locations of winter ranges in Venezuela (95% fixed-kernel) of Turkey Vulture pair T3 male (transmitter 85753, 2009–11) and T4 female (transmitter 85754, 2009–11).

The differences in the sizes of breeding versus wintering ranges may be explained by differences in food availability on the breeding versus wintering grounds, as well as by reproductive obligations at the breeding sites. Site-based differences in food availability may be due to differences (1) in the densities of carcasses available, (2) their rates of decomposition, and (3) the densities of vultures present. We know of no studies comparing the densities of carcasses available in Venezuela versus Saskatchewan, nor are we aware of studies assessing decomposition rates in the two areas. On the other hand, standardized road counts conducted in central Saskatchewan and the Llanos of Venezuela (cf. Bildstein et al. 2007) indicate at least four times as many Turkey Vultures in Venezuela in winter as were seen in Saskatchewan in summer, as well as even greater numbers of Black Vultures in Venezuela versus none in the latter (K. Bildstein and M. Bechard unpubl. data). In addition, migratory vultures wintering in Venezuela do not have the responsibility of raising young and can exploit their ability to travel long distances with minimal energy use. We suggest that the combination of reduced food availability, resulting at least in part from increased densities of avian scavengers, coupled with birds not being ''anchored'' to a nest, are responsible for the substantial increase in wintering range sizes compared to those exhibited in summer. Whatever the reason, the increased geographic mobility we found in overwintering Turkey Vultures mirrors that found in other raptors whose wintering ranges have been studied using satellite tracking (Bildstein 2006), and represents the largest ranges yet reported for the species.

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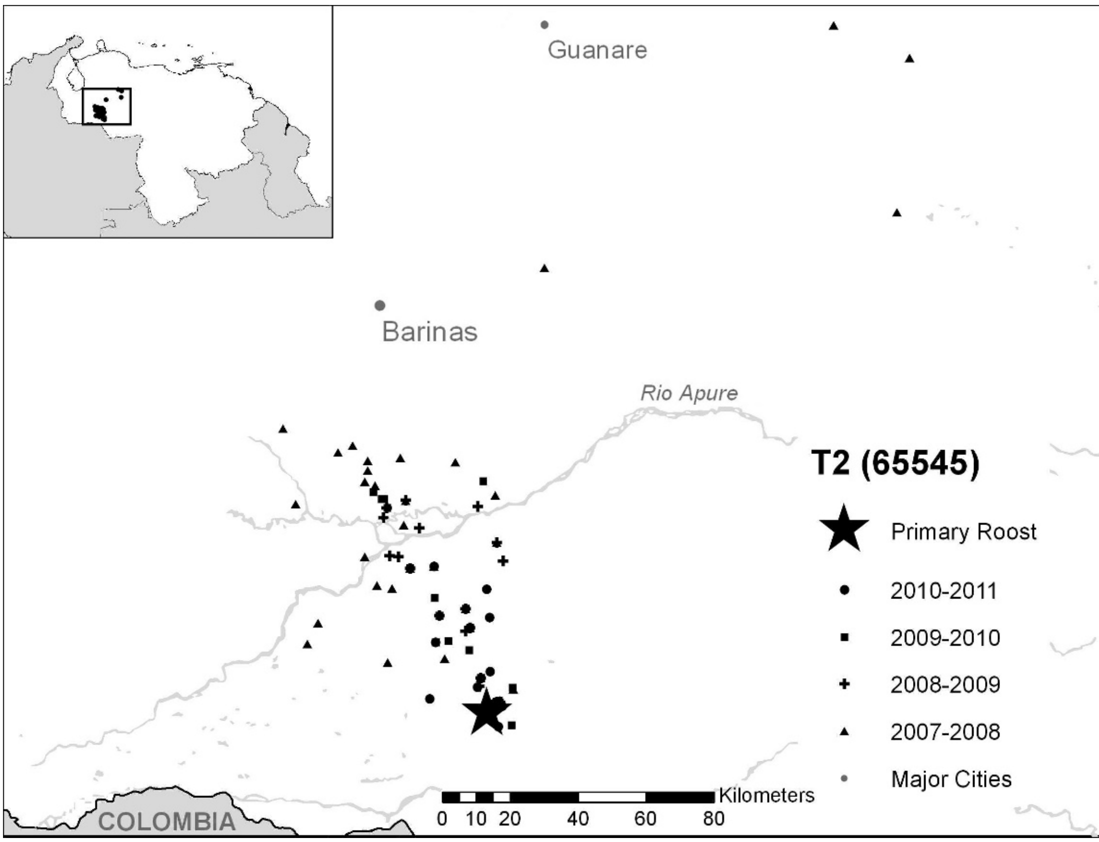

Figure 3. Locations of nocturnal roosts of T2 female in Venezuela (transmitter 65545, 2007–11). The star indicates location of primary nocturnal roost, occupied for 12 to 19 hr on 73, 77, 61 and 92 nights, respectively, in each of four consecutive winters.

that include reporting of five of our wing-tagged birds at the Maracaibo Zoo in northwestern Venezuela, and for assisting M.J. Bechard during his 6-d trip to the southern Llanos. Since 2003, observant and cooperative Saskatchewan farmers have informed us of the locations of over 200 deserted buildings occupied by vultures. The Animal Care Committee, University of Saskatchewan, approved our handling of nesting vultures. This is Hawk Mountain Sanctuary contribution to conservation science number 228.

LITERATURE CITED

ARRINGTON, D.P. 2003. Flight characteristics of non-migrating populations of Turkey Vultures. Ph.D. dissertation. Purdue University, Lafayette, IN U.S.A.

Table 3. Comparison of breeding (Houston et al. 2011) and winter ranges of Turkey Vultures captured in Saskatchewan (SK), Canada, and wintering in Venezuela (VZ).

			AVERAGED 95% KERNELS (km²)	
VULTURE ID	TRANSMITTER	SEX	BREEDING IN SK (YEARS)	NONBREEDING IN VZ (YEARS)
H8	65544	Unk	316 (2007)	167 (2008)
T2	65545	F	567 (2007)	4775 (2007–2011)
T3	85753	M	49 (2009)	65 715 (2009–2011)
T4	85754	F	75 (2009)	318 (2009–2011)
Mean ± SD			252 ± 242	17 743 ± 32 052

BILDSTEIN, K.L. 2006. Migrating raptors of the world: their ecology and conservation. Cornell Univ. Press, Ithaca, NY U.S.A.

———, M.J. BECHARD, P. PORRAS, E. CAMPO, AND C.J. FARMER. 2007. 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. Pages 47–60 *in* K.L. Bildstein, D.R. Barber, and A. Zimmerman [EDS.], Neotropical raptors. Hawk Mountain Sanctuary, Orwigsburg, PA U.S.A.

BOHRER, G., D. BRANDES, J.T. MANDEL, K.L. BILDSTEIN, T.A. MILLER, M. LANZONE, T. KATZNER, C. MAISSONEUVE, AND J.A. TREMBLAY. 2012. Estimating updraft velocity components over large spatial scales: contrasting migration strategies of Golden Eagles and Turkey Vultures. *Ecology Letters* 15:96–103.

BROOK, Q. 2010. Learn Six Sigma and Minitab: the complete toolbox guide for all Learn Six Sigma practitioners. OPEX Resources Limited, Winchester, U.K.

CHAPMAN, F.M. 1933. The migration of turkey buzzards as observed on Barro Colorado Island, Canal Zone. *Auk* 50:30–34.

COLEMAN, J.S. AND J.D. FRASER. 1989. Habitat use and home ranges of Black and Turkey vultures. *Journal of Wildlife Management* 53:782–792.

DEVAULT, T.L., B.D. REINHART, I.L. BRISBIN, AND O.E. RHODES, JR. 2004. Home ranges of sympatric Black and Turkey vultures in South Carolina. *Condor* 106:706–711.

FERGUSON-LEES, D. AND D.A. CHRISTIE. 2001. Raptors of the world. Christopher Helm, London, U.K.

HAMILTON, S.K., S.J. SIPPEL, AND J.M. MELACK. 2002. Comparison of inundation patterns among major South American floodplains. *Journal of Geophysical Research* 107(D20), doi:10.1029/2000JD000306.

HASSELBLAD, K. AND M.J. BECHARD. 2007. Male Northern Goshawk home ranges in the Great Basin of south-central Idaho. *Journal of Raptor Research* 41:150–155.

HOUSTON, C.S., P.D. MCLOUGHLIN, J.T. MANDEL, M.J. BECHARD, M.J. STOFFEL, D.R. BARBER, AND K.L. BILDSTEIN. 2011. Breeding home ranges of migratory Turkey Vultures near their northern limit. *Wilson Journal of Ornithology* 123:472–478.

JENSEN, W.J., M.S. GREGORY, G.A. BALDASSARRE, F.J. VILELLA, AND K.L. BILDSTEIN. 2005. Raptor abundance and distribution in the llanos wetlands of Venezuela. *Journal of Raptor Research* 39:417–428.

KERNOHAN, B.R., R.A. GITZEN, AND J.J. MILLSPAUGH. 2001. Analysis of space use and movements. Pages 125–166 *in* J.J. Millspaugh and J.M. Marzluff [EDS.], Radio tracking and animal populations. Academic Press, San Diego, CA U.S.A.

KIRK, D.A. AND A.G. GOSLER. 1994. Body condition varies with migration and competition in migrant and resident South American vultures. *Auk* 111:933–944.

——— AND M.J. MOSSMAN. 1998. Turkey Vulture (*Cathartes aura*). *In* A. Poole and F. Gill [EDS.], The birds of North America, No. 339. The Academy of Natural Sciences, Philadelphia, PA and the American Ornithologists' Union, Washington, DC U.S.A.

MANDEL, J.T., G. BOHRER, D.W. WINKLER, D.R. BARBER, C.S. HOUSTON, AND K.L. BILDSTEIN. 2011. Migration path annotation: cross-continental study of migration-flight response to environmental conditions. *Ecological Applications* 21:2258–2268.

MCLOUGHLIN, P.D. AND S.H. FERGUSON. 2000. A hierarchical pattern of limiting factors helps explain variation in home range size. *Écoscience* 7:123–130.

MITTERMEIER, R.A., C.G. MITTERMEIER, P.R. GIL, J. PILGRIM, G. FONESCA, T. BROOKS, AND W.R. KONSTANT. 2003. The Llanos. Pages 265–270 *in* R.A. Mittermeier, C.G. Mittermeier, P.R. Gil, and J. Pilgrim [EDS.], Wilderness: earth's last wild places. Conservation International CEMEX de SV, The University of Chicago Press, Chicago, IL U.S.A.

MUNDY, P.J., D. BUTCHART, J. LEDGER, AND D.S. PIPER. 1992. The vultures of Africa. Academic Press, New York, NY U.S.A.

PEERY, M.Z. 2000. Factors affecting interspecies variation in home-range size of raptors. *Auk* 117:511–517.

ROLANDO, A. 2002. On the ecology of home range in birds. *Revue d'Ecologie-La Terre et la Vie* 57:53–73.

SCHOENER, T.W. 1981. An empirically based estimate of home range. *Theoretical Population Biology* 20:281–325.

SWIHART, R.K. AND N.A. SLADE. 1985. Influence of sampling interval on estimates of home-range size. *Journal of Wildlife Management* 49:1019–1025.

VILELLA, F.J., M.S. GREGORY, AND G.A. BALDASSARRE. 2010. Abundance and distribution of waterbirds in the llanos of Venezuela. *Wilson Journal of Ornithology* 122:102–115.

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