BREEDING HOME RANGES OF MIGRATORY TURKEY VULTURES NEAR THEIR NORTHERN LIMIT

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ABSTRACT.—We used Global Positioning System (GPS) satellite transmitters to estimate the breeding home ranges of Turkey Vultures (*Cathartes aura*) in Saskatchewan, Canada from 2005 to 2009. Breeding ranges calculated using 95% Minimum Convex Polygons (MCP) ranged from 47 to 953 km² and averaged (\pm SD) 371 \pm 340 km². Fixed-kernel home ranges (95%) ranged from 49 to 1,992 km² and averaged 648 \pm 731 km². These ranges include both the smallest and largest summer ranges reported for the species. Spatial variation in range size may have been due to differences in availability of food and the quality of the home ranges involved, amplified by the species' extremely low-cost soaring flight. Adults used all-night perches in varying locations up to 38 km from their nest house while traveling substantial distances to available carcasses to obtain food for their young. Identifying home range sizes for Turkey Vultures is a first step toward understanding how the species is increasing and expanding its distribution in Saskatchewan and elsewhere in Canada. *Received 28 May 2010. Accepted 17 January 2011.*

Both Old and New World vultures are obligate scavenging birds (Rea 1983, Kirk and Mossman 1998). The scavenging niche has ecological requirements that differ from those of more predatory raptors (Wilbur and Jackson 1983, Mundy et al. 1992). Feeding on carcasses, which can be highly ephemeral and unpredictable (Kelly et al. 2007), often requires breeding vultures to range widely in search of food for their developing young (e.g., Kirk and Mossman 1998). Turkey Vultures (Cathartes aura) exhibit considerable variation in size of home ranges, both within and among geographic areas. Home ranges of nonbreeding vultures captured at communal roosts varied from 128 to 1,227 km² in southeastern Minnesota (Tenney 1986), 91 to 482 km² in South Carolina (DeVault et al. 2004), 149 km² in Ohio to 627 km² in Indiana (Arrington 2003), and 149 to 371 km² at Gettysburg in southern Pennsylvania and northern Maryland (Coleman and Fraser 1989).

Turkey Vultures breed from Canada to southern South America, adapt well to grasslands, deserts, deciduous and mixed-deciduous forests, and open and forested tropical lowlands: they are the most widely distributed scavenging bird in the world (Wilbur 1983, Ferguson-Lees and Christie 2001). Individuals can be found year-round in the southern United States, but more northerly breeders migrate from breeding areas to overwinter in the southern United States, Central America, and northern South America (Chapman 1933, Stewart 1977, Kirk and Mossman 1998, Mandel et al. 2011). The most northern breeding populations are in western Canada, including central Saskatchewan. This recent expansion of vulture distribution coincided with an increase in use of long-abandoned farm buildings as nesting sites (Houston et al. 2007).

We have few data on the breeding ecology of Turkey Vultures, apart from locations and characteristics of nest sites, near the northern limits of their range. In particular, we know little concerning size of their breeding home ranges. Our objectives were to: (1) document the size of breeding home ranges of Turkey Vultures in central Saskatchewan, and (2) test the hypothesis that size of home ranges near the periphery of their range would be larger than farther south. Macro-ecological theory suggests that, unless there are abrupt changes in habitat types at the limits of a species' range, individuals should be more concentrated at the center of the range than near its boundaries (Brown 1984, 1995), possibly because of higher competition for food (Gross and Price 2000). Thus we initially predicted larger home range sizes for Turkey Vultures than previously reported.

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METHODS

Study Area.-We tracked vultures at four sites in central Saskatchewan, Canada: two in the Aspen Parkland ecoregion (i.e., a transition zone between southern dry grasslands and northern boreal forest) and two in the Southern Boreal Forest ecoregion (below and above 52.5° latitude). Most Aspen Parkland is now cultivated; however, native grasslands and woodlands, respectively, are dominated by fescue grassland (Festuca spp.), and quaking aspen (Populus tremuloides) and balsam poplar (P. balsamifera). The Southern Boreal Forest ecoregion is the most diverse biotic region in Saskatchewan (Smith 1996, Thorpe 1999) with an overstory of mixed deciduous (aspen and balsam poplar) and coniferous trees (white spruce [Picea glauca], black spruce [P. mariana], and jack pine [Pinus banksiana]).

Nest Location and Radio Transmitters.—We used radio and newspaper publicity to contact farmers who believed that Turkey Vultures nested on their property. This was critical as many of the farm buildings occupied by nesting vultures were "hidden" by aspen and caragana (*Caragana* spp.) trees growing in the long-deserted farmsteads.

We captured six adult vultures at their nests and equipped each with an alpha-numeric patagial tag on the right wing and a back-pack style (Steenhof et al. 2007), solar-powered Global Positioning System (GPS) satellite transmitter. We attached four units (#'s 57952, 57953, 65544, and 65545 [Microwave Telemetry, Columbia, MD, USA]), which provided locations almost every hour, to one of the breeding adults at each nest in 2005 and 2007. Two units (#'s 85753 and 85754 [North Star Science and Technology, King George, VA, USA]), providing locations every 3 hrs, were attached to a pair of adults at a single nest in 2009. All six transmitters had an accuracy of \pm 10–15 m. Transmitters for four adult vultures recorded the daily maximum elevation above ground and the time when this occurred. We used DNA from feathers to identify individuals as male or female (Health Gene Laboratories, Toronto, ON, Canada) for a pair of adults captured at the same nest site (male # 85753 and female # 85754),

Breeding Home Ranges.—The 2005 and 2007 migration paths to Venezuela and back appear in Mandel et al. (2011). We used locations after birds returned to Saskatchewan during weeks

when adults were incubating eggs or feeding young (Jun-Aug) to calculate home range size. We used 95% Minimum Convex Polygon (MCP; White and Garrott 1990) and 95% fixed-kernel (Worton 1989, 1995) methods, using the Home Range Estimator (HRE) program of Rogers and Carr (1998) available for ArcView 3.2 (ESRI 2005). The 95% kernel contour is believed to most accurately reflect home range size because it minimizes biases caused by inclusion of outlying locations in the range estimate (Kernohan et al. 2001, Hasselblad and Bechard 2007). GPS telemetry data generated large data sets, including multiple locations (up to 24) on single days. We re-sampled all data sets to 120 randomly chosen points to reduce autocorrelation for computing fixed-kernel home ranges, which are distributions of use sensitive to temporal autocorrelation (Schoener 1981; Swihart and Slade 1985a, b; Ackerman et al. 1990). We computed the smoothing parameter (h) of fixed-kernel ranges as the optimum value with reference to a known standard distribution (i.e., Silverman 1986; Worton 1989, 1995). This was the square root of the mean variance in x and y co-ordinates divided by the sixth root of the number of points following a standard bivariate normal probability density function (Rogers and Carr 1998). We used this method because, after 1 week of brooding, each adult vulture typically visited the nest site once daily, and h-ref is expected to be effective if the underlying use distribution is unimodal (Worton 1995, Roger and Carr 1998). Statistical analyses were performed in R Version 2.10.0 (R Foundation for Statistical Computing 2009). Data presented are mean \pm SD.

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RESULTS

We obtained an average of 988 \pm 392 satellitetracking locations per bird per year (Table 1). Home range size estimated using the 95% MCP method ranged from 47 to 953 km², averaging 371 \pm 340 km² (Table 1). Fixed-kernel home ranges (95%) ranged from 49 to 1,992 km² and averaged 648 \pm 731 km² (Table 1). Fixed-kernel ranges calculated from 120 randomly selected points to minimize temporal autocorrelation in each telemetry location did not differ from fixed-kernel home ranges calculated using all points available for a bird (paired two-sample *t*-test, *t* = -1.32, *P* = 0.23). Mean home-range size calculated using the 95% MCP and 95% fixed-kernel methods also did not differ (paired two-sample *t*-test, *t* = -028,

TABLE 1. Annual breeding home range size of six Turkey Vultures in central Saskatchewan, Canada, 2005–2009. Estimates of 95% fixed-kernel home ranges were based on a random subsample of 120 locations (all birds). ID = patagial tag and transmitter number.

Vulture ID (Year)	Dates	M/F	п	95% MCP (km2)	95% Fixed Kernel (km ²)
H2 57952 (2005)	19 Jun-13 Aug	Unk	945	953	1,992
H0 57953 (2005)	19 Jun-18 Aug	Unk	1,217	502	891
H8 65544 (2007)	18 Jun-18 Aug	Unk	1,342	261	316
T2 65545 (2007)	17 Jun-19 Aug	Unk	1,320	416	567
T3 85753 (2009)	22 May-28 Aug	М	331	47	49
T4 85754 (2009)	22 May-28 Aug	F	774	47	75
Mean \pm SD			988 ± 392	371 ± 340	$648~\pm~731$

P = 0.98). Home ranges decreased in size from 2005 to 2009 (fixed-kernel home range size vs. year, t = 3.98, P = 0.016, $r^2 = 0.80$) (Table 1).

We received good signal reception during early incubation, 23-30 May for the pair of adults captured at the same nest site (male # 85753 and female # 85754), and for the female during brooding, 30 June-4 July (Figs. 2, 3). Transmitter signals were not received from male # 85753 throughout most of June and the entire brooding period in early July. Both adults took turns incubating until the eggs hatched between 25 and 30 June (Fig. 2); brooding then became intensive by the female for about 18 hrs per day including each night through 4 July (Fig. 3). Brooding ceased entirely after 10 July and a daily feeding visit by each adult was so brief that it was rarely recorded near the nest house. All-night perch sites, rarely used more than once, after brooding ceased, were unexpectedly distant for all 6 adults: up to 37.8, 38.8, 14.5, 29.7, 7.5, and 15.9 km from the nest house with young (Table 2). Vultures ascended to 558, 902, 681, and 627 m above the altitude of the nest house when searching for carcasses (Table 3).

DISCUSSION

There was considerable variation in breeding home range size of the Turkey Vultures we tracked; we recorded some of the smallest and largest breeding ranges recorded for the species. What governs home range size can be complex (McLoughlin and Ferguson 2000, Peerv 2000): however, a wide-ranging survey of home range size in birds (Rolando 2002) suggests food availability is the primary determinant of avian range size and all other factors are secondary. We suggest heterogeneity in food availability may explain variation in the breeding range size for the vultures we studied. For example, the small breeding range sizes of vultures # 85753 and # 85754, a mated pair tracked in 2009, were in the North Saskatchewan River Valley (Fig. 1), a relatively productive riparian area; these vultures may have had greater access to food than the other four birds in our study. It also is possible that carrion availability changed among years, as we observed larger breeding ranges earlier in the 4year study than in later years. Large home range sizes are made possible, in part, by the species' extremely low-cost soaring flight (cf. Mandel et

TABLE 2. Night perches of six Turkey Vultures occupying home ranges in central Saskatchewan, Canada, 2005–2009. Distances (km) are from the known nest house to all-night perch sites.

H0	H2	H8	T2	T3 male	754 6 1
			12	15 male	T4 female
57953	57952	65544	65545	85753	85754
61	52	61	64	99	99
61	52	58	60	34	79
0	0	0	0	5	20
37.8	38.8	17.7	29.7	7.5	15.9
8.2	21	5.6	8.1	2.3	2.4
0.62	1.5	0.8	1.1	1.2	0.25
	61 61 0 37.8 8.2	61 52 61 52 0 0 37.8 38.8 8.2 21	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	$\begin{array}{cccccccccccccccccccccccccccccccccccc$	

Patagial tag	H0	H2	H8	T2		
Transmitter #	57953	57952	65544	65545	Totals	% Total
Total days	61	52	61	64	238	
Days <99 m elevation above nest house	31	21	26	17	95	40
Days >100 m elevation above nest house	30	31	35	47	143	60
Highest flight (m) above nest house	558	902	681	627		
Date of highest flight	10 Jul	4 Aug	6 Jul	12 Jul		
Mean height of flights >100 m	265	405	309	304		
Mean height of all daily highest flights (m)	152	252	197	233		
Hours of highest flight (CST):						
1000	1	1		2	4	3
1100	7	4	4	3	18	12
1200	3	5	6	3	17	12
1300	5	3	7	8	23	16
1400	5	5	8	10	28	19
1500	5	1	5	11	22	15
1600	1	6	5	5	17	12
1700	1	4	2	5	12	8
1800	2	1		1	4	3
1900		1			1	1
Totals	30	31	37	48	145	101
Mean time (CST) of highest flight	1324	1429	1343	1411		

TABLE 3. Soaring flight characteristics for four Turkey Vultures occupying home ranges in central Saskatchewan, Canada, 2005–2007.

al. 2008, 2011), which significantly reduces the cost of searching large areas for carrion.

We found published records of only three vultures for which breeding home ranges were calculated. The two vultures tracked during the breeding season near Gettysburg had 95% MCP home ranges with a mean of either 69.4 km² (Coleman and Fraser 1989) or 126.0 km² (Coleman 1985). Arrington (2003) captured one adult female vulture on her nest at the Pigeon River Wildlife Area, northeastern Indiana; it had a 100% MCP of 557 km² and a 90% kernel of 9.9 km² based on 342 satellite transmitter readings. Our mean 95% MCP of 371 km² was similar. The size of our Saskatchewan home breeding ranges was uniquely limited to locations of known breeding vultures from incubation through fledging of young. Comparisons with other studies of the home-range size of nonbreeding Turkey Vultures (e.g., Tenney 1986, and those studied by Coleman and Fraser 1989 and DeVault et al. 2004) are less appropriate.

Tracking both members of a pair of Turkey Vultures (male # 85753 and female # 85754) during incubation and brooding provided new information. Both had relatively small and virtually identical home ranges. Each would incubate for either one or two consecutive nights when regular signals were received from both during 23–30 May (Fig. 2). However, brooding was exclusively by the female at night during 30 June–4 July, but with 6 hrs respite in mid-day (Fig. 3); signals were not received from the male during this time. Brooding by the female ceased after 27 hrs of continuous brooding on a notably cool and rainy day, 10 July (data from Environment Canada, http://climate.weatheroffice.gc.ca).

Identifying size of home ranges for Turkey Vultures near their northern range limits increases our understanding of how the species is adapting to recently occupied areas in Saskatchewan and elsewhere in Canada. We believe the recent human depopulation of rural areas, together with abandonment of farm buildings, has had a crucial role in increasing numbers of successfully nesting Turkey Vultures. Vulture nests were rarely discovered prior to the 1980s, and were restricted to difficult-to-find caves in badlands in extreme southern Saskatchewan and along major river valleys through southern and central Saskatchewan with occasional single-year use of cavities within large brush-piles. Northward range extension is not involved, but in 1982-1984, the first four vulture pairs were found in deserted buildings in central Saskatchewan and vultures were no longer relying on natural caves for nesting

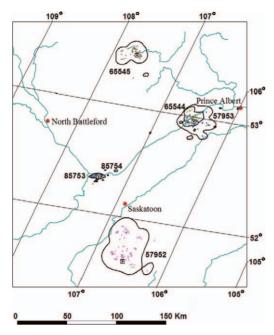


FIG. 1. Telemetry locations and annual breeding home ranges (95% fixed-kernel) of six Turkey Vultures (satellite identification number indicated) in central Saskatchewan, Canada, 2005–2009. Nest sites (abandoned buildings) are indicated as dotted squares. Vultures # 57953 and # 65544 shared the same site in different years; vultures # 85753 and # 85754 were a mated pair.

(Houston et al. 2007). Vultures were soon breeding widely in deserted buildings on farms throughout the Aspen Parkland and southern Boreal Forest ecoregions (Houston and Terry 2003). For example, vultures first nested in the 11,012 km² Saskatoon Bird Area in 2002 (Houston et al. 2002) and most farmers in Saskatchewan have reported vultures only during the past decade.

These increases in vulture nesting activity may also be in response to gradual increases in availability of ungulate carrion, related to documented province- and Canada-wide increases in wildlife-vehicle collisions (especially with deer) on highways (Tardif and Associates 2003). The number of reported collisions with wildlife in Saskatchewan from 1988 to 2009 increased from 3,695 to 13,052 with a particularly marked rise in the past decade (Traffic Information System, Saskatchewan Government Insurance, Regina, Canada). Short-term increases in carrion supply are also coincident with management actions, enacted in 2002, to control Bovine Spongioform Encephalopathy (BSE); these actions closed

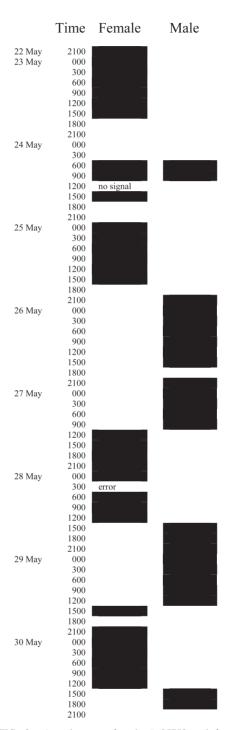


FIG. 2. Attentiveness of male # 85753 and female # 85754 during early incubation, 23–30 May 2009. Black = present at nest site.

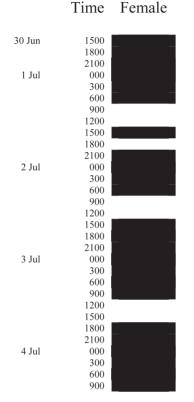


FIG. 3. Attentiveness of female # 85754 while brooding downy young, 30 June–4 July 2009. Black = present at nest site.

export markets and increased slaughter and disposal of non-saleable older livestock at farmsteads (Dunn 2004). The average fed steer price in Saskatchewan in 2007–2008 fell below production costs to \$84 per hundred-weight, only half the 1942–1989 inflation-adjusted average price (National Farmers Union 2008).

The lack of a substantial increase in the breeding home range size of Turkey Vultures near the northern limits of its range suggests food resources there are not appreciably different from those farther south. It is also possible these limits are set by distances the birds travel twice annually to and from southern wintering areas (*cf.* Mandel et al. 2008, 2011). "Western North America populations of Turkey Vultures forego feeding *en route*, at least for most of their journey" (Bildstein 2006:191) and "the condition of adult migrants [in Venezuela] was below average in October and November following migration from the breeding grounds" (Kirk and Gosler 1994: 933). Physiological and aerodynamic constraints

on fat loading prior to migration may preclude longer seasonal movements. Studies of the size of breeding home ranges of Turkey Vultures, especially in the Neotropics of Central America, northern South America, and the temperate zone of southern South America, are warranted.

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