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POPULATION AND MOVEMENT CHARACTERISTICS OF RADIO-COLLARED STRIPED SKUNKS IN NORTH DAKOTA DURING AN EPIZOOTIC OF RABIES

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ABSTRACT: We observed a total of 102 striped skunks (*Mephitis mephitis*) from March to July of both 1991 and 1992 in Stutsman County, North Dakota (USA) during an experiment with food supplementation. Twenty-three apparently healthy skunks in 1991 and 56 in 1992 were equipped with radio-collars. In 1991, one of the 23 was tested and found to be rabid. In 1992, 50 of 56 were tested; 35 (70%) were rabid. Of skunks with ages estimated, 19 (66%) of 29 were first year animals in 1991 compared with nine (22%) of 41 first year animals in 1992. All 18 females captured in 1991 were pregnant or parous compared with 21 (60%) of 35 in 1992. The estimated survival rate of skunks was 0.85 during April to June 1991, but only 0.17 during April to July 1992. In 1992, the survival rate of first year skunks was 0.08, compared with 0.35 for older animals. Eleven (31%) of 36 skunks found dead of rabies or in late clinical stage were located below ground. We detected no differences in 1992 between healthy and rabid skunks in estimated mean (±SE) rate of travel (232 ± 14 m/hr), distance traveled (2,047 ± 141 m/night), or home range size (1.6 ± 0.4 km^2) during half-month periods from April through June. Among rabid skunks, mean rate of travel tended to decrease from 298 ± 48 m/hr during the 14 days preceding the clinical period of rabies (pre-clinical) to 174 ± 48 m/hr during the clinical period of rabies (14 days immediately before death). Similar decrease occurred in distance traveled in a night (2,318 ± 281 m, pre-clinical; 1,497 ± 281 m, clinical). Mean home range size of males (2.8 ± 0.4) was greater than of females (1.2 ± 0.4) during the pre-clinical period, but during the clinical period home range sizes of males (1.8 ± 0.4) and females (1.8 ± 0.4) were similar. Mean home range size of females did not differ between pre-clinical (1.2 ± 0.4) and clinical (1.8 ± 0.4) periods ($P = 0.22$). Deaths of skunks from rabies in 1992 tended to be more spatially clumped than expected had they been random, mostly due to deaths detected before 8 May. We detected no correlation between locations of animals found dead of rabies and dates of death.

Key words: Distance traveled, epizootiology, home range, *Mephitis mephitis*, North Dakota, rabies epizootic, radio-telemetry, striped skunk, survival rate, travel rate.

INTRODUCTION

The striped skunk (*Mephitis mephitis*) is the primary species in which rabies is enzootic in midcontinent North America (Charlton et al., 1991). In 1992, skunks accounted for 27% of reported cases of rabies in wild animals in the United States and 20% of all reported cases of rabies in Canada (Krebs et al., 1993). Despite the considerable knowledge about some aspects of rabies (Baer, 1991), only crude estimates of the incidence of rabies in wild animals are available. Infected wild animals are rarely observed; only those submitted to health departments or other diagnostic facilities are included in surveillance reports (Krebs et al., 1993). Charlton et al. (1991) stated that during the clinical period, rabid skunks in captivity may have increased alertness, heightened activity, and aggressive behavior characterized by biting and lack of fear. Little is known, however, about wild animals infected with rabies. Sargeant et al. (1982) demonstrated that interactions and dispersal of striped skunks facilitated transmission of rabies. Murray and Seward (1992) suggested that additional information on rabies in wild animals would be useful in development of control methods.

During both 1991 and 1992, we equipped adult striped skunks with radio-collars in eastcentral North Dakota (USA) as part of an evaluation of skunk responses to supplemental feeding. Provision of supplemental food was suggested by Crabtree and Wolfe (1988) as a potential method of reducing depredation by skunks on eggs of ground-nesting birds. We proposed to evaluate movements of skunks in the prairie region in response to supplemental feeding during the waterfowl nesting season. In 1991, we detected rabies in one radio-collared skunk, but others were not tested because they appeared to be healthy. In mid-April 1992, we became aware of a potential epizootic of rabies in our study population. Although the epizootic confounded the food provisioning study, the radio-equipped animals afforded us a unique opportunity to observe a population of wild striped skunks during an epizootic of rabies. Thus, we continued to radio-equip and monitor skunks; we captured new skunks periodically to maintain as large a sample of radio-equipped animals as we could monitor. Our purpose is to provide information on the population of skunks we studied during the rabies epizootic and to contrast observations of animals that contracted rabies with those of animals that remained healthy.

In this report we compare age structure, reproductive rate, and survival rate of populations we studied in 1991 and 1992. For the 1992 population, we compare rates of travel, distances traveled, and home ranges of skunks that died of rabies and healthy skunks. We also describe condition and location of skunks that we found dead or dying, temporal and spatial relations among skunks that died of rabies, evidence of interactions among animals, and skunk responses to feeding sites.

MATERIAL AND METHODS

The study was conducted 50 km north of Jamestown, Stutsman County, North Dakota in the Southern Drift Plain of the Prairie Pothole Region (98°52′N, 47°12′W). Landscape of this area is gently rolling and was nearly two-thirds cropland; remaining land was mostly grassland and wetlands. The study area was about 93 km^2 and contained 15 occupied farmsteads. The Arrowwood National Wildlife Refuge managed by the U.S. Fish and Wildlife Service is located along the entire east side of the study area, intersected by the James River. Drought conditions prevailed during 1991 and 1992, and except for the James River and a few impoundments and spring-fed dugouts for livestock, most wetlands in the study area were dry.

We captured striped skunks in livetraps (24 × 24 × 66 cm) (Tomahawk Live Trap Company, Tomahawk, Wisconsin, USA) and anesthetized them with 0.75 to 1.0 ml of a premixed combination of 60 mg ketamine HCL (Fort Dodge Laboratories, Fort Dodge, Iowa, USA) and 15 mg xylazine HCL (Mobay Corporation, Animal Health Division, Shawnee, Kansas, USA) per ml (Crabtree and Wolfe, 1988). We placed animals in shade near the capture site for recovery. If euthanasia was necessary, we administered a combination of pentobarbital sodium (390 mg/ml) and phenytoin sodium (50 mg/ml) (Shering-Plough Animal Health Corporation, Kenilworth, New Jersey, USA) after anesthesia. These and all other protocols were approved by the Northern Prairie Science Center Animal Care and Use Committee and followed recommendations of The American Society of Mammalogists (1987). Field personnel who handled skunks had received prophylactic rabies immunization.

In 1991, we captured skunks in the interior 44 km^2 of the study area so we could test experimental protocols of the food provisioning study. Capture was primarily on two occasions (18 to 20 April and 21 to 31 May). We recaptured and euthanized animals approximately 3 to 4 wk after capture so we could remove those that had been tested from the population and so we could determine animal ages.

In 1992, we captured skunks throughout the 93-km^2 study area, primarily during 31 March to 5 April. We trapped and equipped new skunks with radio transmitters on several occasions to replace animals that died and maintain sufficient marked animals for population monitoring. In mid-July, to permit age determination and testing for rabies, we euthanized and retrieved all radio-collared skunks and some unmarked skunks captured at sites where we provided supplemental food (hereafter called feeding sites). During both years, all nontarget animals were released unharmed.

At initial capture we determined the sex of each skunk and placed a numbered tag (1 × 3 mm) in each ear. At the same time we attached an approximately 60 g radio-collar (164 to 167 Mhz) (Advanced Telemetry Systems, Inc., Isanti, Minnesota, USA) detectable up to 3.2 km; collars contained a motion-sensor that permitted us to identify mortality (animal motionless for ≥3 hr). We noted and recorded obvious scars and bite marks on skunks each time an animal was anesthetized. We examined live females for pregnancy by palpation and conducted post mortem examinations for fetal swellings or fresh uterine implantation sites; lactation also was interpreted as evidence of pregnancy in the current year. We estimated skunk ages post mortem to the nearest year by counting annuli in canine teeth (Johnston and Watt, 1981).

In 1992, we provided foods (chicken eggs, dry dog food, fish, sunflower seeds) and an attractant (fatty acid scent disk, U.S. Fish and Wildlife Service, Pocatello Supply Depot, Pocatello, Idaho, USA) at 10 permanent feeding sites established ≥3.2 km apart (Fig. 1). Each site was composed of four 1-m-diameter plots (20 m apart in a row) where foods and lure were provided continuously from 1 April to 9 July. Foods were replenished daily between 0800 and 1500 and the attractant was replaced every 3 to 4 wk. Sites were in idle grassland ≥50 m from the nearest road to avoid disturbance by humans.

Observers determined locations of radio-collared skunks by triangulation from vehicles equipped with null-peak antenna systems. Locations were plotted immediately on a 1:24,000 map and converted later to universal transmercator (UTM) coordinates. Locations were not recorded during the first 10 to 12 hr after each occasion when a skunk was anesthetized. Accuracy of locations was confirmed by sightings of radio-equipped animals (Fenn and Macdonald, 1995) and during visits to retreats occupied by skunks and locations of carcasses; accuracy was usually within 50 m.

We located skunks once each day between 0700 and 1800 to determine their diurnal retreats (hereafter called day-tracking). We located skunks at 2-hr intervals between 1800 and 0700 the next morning to determine their nocturnal movements (hereafter called night-tracking). During 18 April to 20 June 1991, we conducted day- and night-tracking irregularly while we tested study protocols. From 15 April to 9 July 1992, we systematically conducted day-tracking on 6 of every 7 days and night-tracking on 5 nights every half month. Nights were preselected at the beginning of each half-month period to distribute tracking effort throughout the period. During night-tracking, two observers each monitored one half of the radio-collared skunks. Any radio-collared skunk that was not located during day- or night-tracking was sought continuously during all tracking efforts, including occasional searches outside the study area. Animals that dispersed from the study area were recaptured when found, and euthanized.

Skunks suspected of being sick or dead, based on radio-signal or unusual location, were checked promptly the next morning by an observer on foot with a hand-held radio-receiver. Skunks found alive but immobile were euthanized.

In 1992, euthanized skunks and those found dead were transported to Jamestown for necropsy. Upper canine teeth were removed and frozen until used to estimate animal age. Brains were removed, placed in individual identified containers, and shipped under refrigeration to the North Dakota State University Veterinary Diagnostic Laboratory.

One half of each brain was fixed in 10% buffered formalin, stained with hematoxylin and eosin (H&E), and examined by light microscopy. Impression smears were made from the unfixed half of the brain, stained with fluorescein labelled antibody (FA), and examined by fluorescent microscopy (Velleca and Forrester, 1981). A positive diagnosis for rabies was based on a positive FA test, with or without the presence of lesions on the H&E-stained slides.

Brains with lesions of viral or lymphocytic encephalitis, but negative for rabies antigen by the FA test, were injected intracranially into anesthetized mice. Brain tissue from treated mice was subjected to FA testing. Skunks positive for rabies by mouse inoculation test were included with others diagnosed as positive. Hereafter, we refer to skunks that tested positive for rabies antigen as rabid skunks and to those in which we did not detect rabies antigen as healthy skunks.

For animals in which we did not detect rabies antigen in mouse brain tissue by the FA test, the original skunk brain was tested again in an attempt to determine etiology of the lesions. The fixed sections were immunohistochemically stained for morbillivirus antigens using a rabbit polyclonal antisera to human measles virus nucleoprotein and an aviden-biotin complex technique (Haines and Clark, 1991).

We grouped skunks into three classes by age: age class 1, <2-yr-old; age class 2, ≥2-yr-old and <3-yr-old; age class 3, ≥3-yr-old. Grouping reduced the effect of errors in age estimation, which tend to increase with animal age (Johnston et al., 1987) and also reduced statistical problems associated with small samples. We contrasted, by sex and age class, proportions of skunks captured during 1991 and 1992 with a larger sample of striped skunks obtained during the months of April to July, 1979 through 1990 in similar habitats of east central North Dakota and west central Minnesota (Greenwood and Sargeant, 1994). We tested, with chi-square statistics, the effects of year (1979 through 1990, 1991, 1992), sex, and year by sex interaction on age class of skunks, using weighted least-squares estimation techniques (Grizzle et al.,

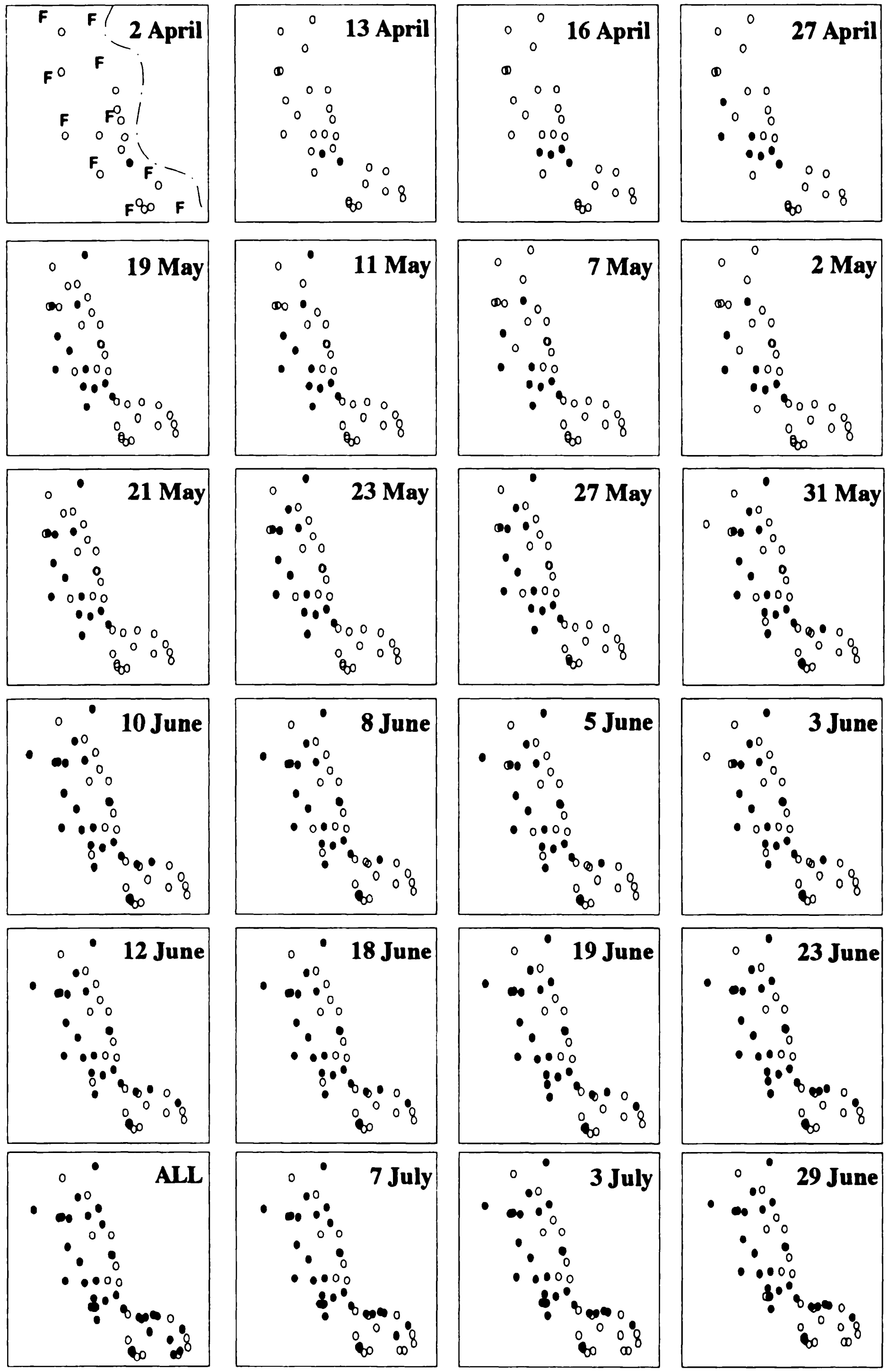

FIGURE 1. Feeding sites (F) and activity centers (circle) of radio-collared striped skunks in Stutsman County, North Dakota, 31 March to 15 July 1992. Each circle represents the mean universal transmercator grid coordinate for a skunk, based on all capture and radio-telemetry locations for that animal. Number of circles is the total number of radio-collared skunks monitored as of date shown in upper right corner of plot. Solid circle represents rabid skunk that died. Location of James River is depicted by dashed line in plot dated 2 April.

1969) with the procedure CATMOD (SAS Institute, Inc., 1989a). Pairwise comparisons were conducted for significant effects using contrast statements in the procedure CATMOD. Throughout this report, variation is expressed as standard error ($\bar{x} \pm$ SE); differences are considered significant at $P = 0.05$.

We estimated survival rates ($\hat{S}$) of radio-collared skunks for 1991 and 1992 with Kaplan-Meier estimation techniques in a staggered entry design (Pollock et al., 1989). We computed mortality rates due to three specific causes: rabies, suspected predation by carnivores (includes some rabid skunks), and other; other included vehicle collisions, shooting, and unknown causes. We censored (Lee, 1992) observations of healthy skunks on the date they were euthanized. For this analysis, to compensate for small sample sizes in some categories, we combined age class 3 with age class 2. We then compared $\hat{S}$ between sexes and age classes (1 and 2) using the procedure IML (SAS Institute, Inc., 1989a) following the methods described by Sauer and Williams (1989); we considered the day of capture to be the first day an animal was at risk. We assumed that the variance of $\hat{S}$, when $\hat{S} = 1.00$, was equal to a pooled group estimate.

Because skunks may have heightened levels of activity when rabid (Charlton et al., 1991), we examined characteristics of movement and use of space to see if we could detect differences between healthy and rabid radio-collared skunks in 1992. For individual animals, we estimated minimum rate of travel in a night, minimum distance traveled in a night, and minimum size of home range for approximate half-month periods from mid-April to mid-July: period 2, 19 April to 2 May; period 3, 3 to 15 May; period 4, 16 to 29 May; period 5, 30 May to 12 June; period 6, 13 to 25 June; period 7, 26 June to 11 July. We did not derive estimates for animals in 1991, or for period 1 (1 to 18 April) in 1992, because radio-tracking records were incomplete. We used least-squares means and their standard errors (Milliken and Johnson, 1984) to estimate population means; least-squares means are unbiased estimates of population means.

Rate of travel (m/hr) for a skunk was estimated as the distance (m) between two consecutive locations during night-tracking divided by the intervening time interval (hr). We estimated the minimum rate of travel for each radio-collared skunk for which we obtained two or more consecutive locations separated by ≥ 1 but ≤ 3 hr after it left its daytime retreat. On each night for each skunk that met these criteria, we pooled rates for individual pairs of locations and divided the pooled rate by the number of pairs of locations that night for that skunk. We pooled the estimated mean rate of travel per night for each half-month period and divided the pooled mean by the number of nights tracked within each half-month period for each animal.

Distance traveled (m/night) was estimated as the sum of the distances between consecutive locations during night-tracking. We estimated the minimum distance traveled in a night for each skunk that was tracked through a complete night (located in every 2-hr interval) after it departed its daytime retreat until it reached its daytime retreat the following morning. For each animal that met this criterion, we pooled the estimated distances traveled each night for each half-month period and divided the pooled distance by the number of nights to estimate the mean minimum distance traveled per night during a half-month period.

We estimated home range size (km^2) by the minimum area method (Mohr, 1947), using SAS code reported in White and Garrott (1990). We estimated home range size for each animal for each half-month period, based on all capture and radio-tracking locations during that period. We pooled the estimates of home range size for each half-month period and divided the pooled estimate by the number of periods to estimate the mean half-month home range size.

We assessed effects of sex, half-month period, and their interactions on estimated rates of travel, distances traveled, and home range sizes of healthy and rabid skunks with a repeated measures analysis of variance (ANOVA) technique and the general linear models procedure (GLM) (SAS Institute, Inc., 1989a). Animal within sex was the whole unit, and the same animal at different half-month periods (periods 2 through 6) was the subunit (Milliken and Johnson, 1984). We compared estimates only for half-month periods 2 through 6, because we had no data for period 7 for rabid males. For the home range ANOVA, we weighted estimates for each half-month period by the square root of number of locations for that period, to compensate for differences in sample sizes. Home range size tends to increase with number of locations (White and Garrott, 1990), and there was a slight correlation between home range size and number of locations ($r = 0.3$, $P < 0.01$). We used Fisher's protected least significant difference (LSD) (Milliken and Johnson, 1984) to make pairwise comparisons among means for significant main effects.

We were interested in determining if there was more variation in rates of travel among individual skunks, among nights, or within nights throughout the summer. We evaluated sources of variation in observed rates of travel for each combination of sex and rabies status of an animal (rabid or healthy), using a variance component approach (Box et al., 1978). The design was a nested structure (Box et al., 1978) in which rates of travel were estimated at multiple times within each night for individual skunks, across multiple nights for individual skunks, and among individual skunks. Our primary interest was to examine the percent of variation explained by each component relative to the total variation for each combination. We were not interested in testing for differences in variance components among combinations of sex and rabies status. We used the MIVQUE0 method of procedure PROC VARCOMP of SAS (SAS Institute, Inc., 1989a) to compute variance components.

We attempted to isolate effects of rabies on movements of skunks during the clinical period, which we defined as the 14 days preceding death or euthanasia of an immobile animal. Charlton et al. (1984) observed a mean (±SD) duration of the clinical period of 9.7 ± 3.0 days in rabid captive skunks, but in wild skunks this stage was less clearly defined and ranged from 1 to 18 days (Charlton et al., 1991).

We computed the minimum rate of travel, minimum distance traveled, and home range for rabid skunks for the 14-day interval preceding death (hereafter called clinical period) and the previous 14 days (hereafter called pre-clinical period). We pooled results by 14-day intervals and computed means for those intervals.

We used an ANOVA to assess effects of sex, period (pre-clinical or clinical), and their interaction on estimated parameters of travel and home range size. We used the GLM procedure in a repeated measures design (Milliken and Johnson, 1984). Animal within sex was the whole unit and the same animal at different periods (pre-clinical or clinical) was the subunit. If we detected no significant interaction among main effects, we used Fisher's protected LSD (Milliken and Johnson, 1984) to make pairwise comparisons among means for significant main effects. This method of computation permitted us to standardize effects in relation to the clinical period of rabies, which was our primary objective; however, it reduced our ability to examine seasonal effects of rabies. We limited this analysis to animals observed continuously for more than 28 days.

We evaluated the locations of deaths among rabid skunks in 1992 to determine if deaths were random or clumped among the radio-collared population. We included in this analysis all rabid skunks found dead, skunks that we discovered immobile in the late clinical stage of rabies, and skunks with rabies that we believed were killed by predators. We calculated a single location (hereafter called activity center) that represented the home range of each radio-collared skunk tested for rabies. The activity center was based on the mean UTM coordinates of all capture and radio-telemetry locations of each animal for the entire time we monitored it. On each day that we found at least one skunk dead from rabies (hereafter called death-day), we plotted the activity centers of all skunks captured to that day and identified all skunks with rabies when they died.

We tested the hypothesis that the observed spatial pattern of deaths among rabid skunks was random at each death-day, and across all death-days, by using a procedure described in Manly (1991). We computed the distance to the nearest neighbor (hereafter called nearest-neighbor distance) among all dead rabid skunks at each death-day and the mean of those distances. Then, keeping the location fixed of the first skunk to have died with rabies on the first death-day, we computed for each subsequent death-day a distribution of 1,000 mean nearest-neighbor statistics by randomly assigning all dead rabid skunks among all known locations for all skunks to that day (beginning with death-day = 2). The number of skunks randomly-assigned at each death-day equaled the number observed to that date. Next, by averaging across all death-days, we computed the overall mean nearest-neighbor distance for the observed and the randomized distributions. To test the hypothesis, we computed the percentage of mean nearest-neighbor statistics from the randomized distribution that were equal to or greater than the observed mean nearest-neighbor statistic. We used the IML procedure of SAS (SAS Institute, Inc., 1989b) to conduct the randomization testing procedure.

We further evaluated relations among locations of skunks that died of rabies in 1992 with Mantel's test method (Manly, 1991). We tested the hypothesis that skunks whose activity centers were close together spatially would also have dates of death that were close together temporally. To do this, we computed for all skunks that died of rabies (found dead, immobile, and killed by predator) a spatial-distance matrix of all possible pairs of distances between activity centers and a time-distance matrix of all possible pairs of dates of deaths. We then computed a Pearson correlation coefficient (r) by pairing, on an element-by-element basis, the spatial-distance matrix and the time-distance matrix. We computed a randomized distribution of r-values by randomly assigning the spatial-distances to the time-distances 1,000 times. Then, we computed the percentage of r-values from the random distribution that exceeded r-values from the observed distribution. We used the IML procedure of SAS (SAS Institute, Inc., 1989b) to conduct the randomization testing procedure.

We determined the number of times individual radio-collared skunks were observed at feeding sites during night tracking as a percentage of the total number of times they were relocated away from their daytime retreats. Mean values were computed, weighted by the square root of the number of relocations. We used an ANOVA to assess the relationship of sex, rabies, and their interaction to estimated percent of time in a night that skunks were found at feeding sites. We also determined if any skunk visited more than one feeding site during the monitoring period or if more than one skunk was at an individual feeding site at the same time.

RESULTS

We observed 31 adult striped skunks in 1991. Twelve females and 12 males were captured during April or May; one female died at capture and 23 were equipped with radio-collars. Six females and one male captured at feeding sites in late June were not equipped with radios. Radio-tracking was conducted from 17 April to 19 June. Two animals were monitored for only ≤4 days (one female was shot; one male dispersed). We obtained a mean of 74 (range, 64 to 91) locations of the remaining 21 animals, including a second male that dispersed 6.9 km between 0100 and 1800 on 20 May; it was collected 8.5 km from its capture location. One aggressive radio-equipped skunk was euthanized and found positive for rabies antigen by FA test.

We observed 62 adult striped skunks in 1992. Thirty-three females and 24 males were captured during March through June; one male died at capture and 56 were equipped with radio-collars. One female and three males captured at feeding sites in mid-July and one female found dead in June were not equipped with radios. Radio-tracking was conducted from 31 March to 15 July. Four radio-equipped animals (two males and two females) died before systematic monitoring began. We obtained a mean of 111 (range, 11 to 296) locations of the 52 radio-collared skunks; 11 of the 52 were located 215 to 296 times. Thirty-six (68%) of 53 skunks (some without radio-collars) were positive for rabies antigen by the FA test. Four additional skunks with lymphocytic meningitis were negative for rabies antigen by FA test. Those four also were negative for rabies by the mouse inoculation test and negative for canine distemper and other morbillivirus antigens by the immunohistochemical test.

We estimated ages of 29 skunks in 1991 and 41 skunks in 1992 (Table 1). Ages of 18 skunks (one with rabies in 1991 and the first 17 found dead or euthanized in 1992) were not estimated because of concern over risk of collecting teeth from potentially rabid animals. Among animals with ages estimated, we detected no year by sex interaction effect (chi-square = 2.71; df = 4; $P = 0.61$) or sex main effect (chi-square = 2.48; df = 2; $P = 0.29$); thus differences in proportions of skunks by age class among years appeared similar for males and females. We detected a significant main effect due to year (chi-square = 53.61; df = 4; $P < 0.0001$). In 1992, a smaller proportion of skunks comprised age class 1 and larger proportions comprised age classes 2 and 3 than in the years 1979 through 1990 or 1991 ($P < 0.05$) (Table 2). We detected no differences in proportions of skunks between years 1979 through 1990 versus 1991 for age classes 2 or 3 ($P > 0.05$).

In 1991, all 18 females were pregnant or parous. In 1992, 21 (60%) of 35 females were pregnant or parous; nine (26%) had no evidence of recent pregnancy and the status of five (14%) was not determined. Of the 21 reproductively active females in 1992, 12 were positive for rabies and nine were negative; one of the 12 was about 30 days pregnant on 7 July. Of the nine females with no evidence of pregnancy, six were positive for rabies and three were negative. Two litters were born to the nine females that tested negative for rabies. Two other lactating females were positive for rabies, but litters were not observed before the females died. Based on behav-

TABLE 1. Distribution by age class[a] and sex of striped skunks captured in March–July in east central North Dakota and west central Minnesota during 1979 through 1990[b] and Stutsman County, North Dakota during 1991 and 1992.

			Age class					
			1		2		3	
Year	Sex	Number	Number	%	Number	%	Number	%
1979–1990	Male	208	155	75	41	20	12	6
	Female	155	115	74	22	14	18	12
	Total	363	270	74	63	17	30	8
1991	Male	13	10	77	2	15	1	8
	Female	16	9	56	3	19	4	25
	Total	29	19	66	5	17	5	17
1992	Male	17	5	29	5	29	7	41
	Female	24	4	17	10	42	10	42
	Total	41	9	22	15	37	17	41

[a] Age class 1, <2-yr-old; age class 2, ≥2-yr-old and <3-yr-old; age class 3, ≥3-yr-old.
[b] Capture locations in 1979 through 1990 given in Greenwood and Sargeant (1994).

ior, another female positive for rabies also may have had a litter, but when found dead she was not lactating and apparently no longer had young.

In 1992, five skunks found in late clinical stage of rabies and carcasses of 21 others, including one skunk represented only by a chewed radio-collar, were found above ground (Table 3). Carcasses or remains of 11 skunks were in burrows; an additional three heads with attached radio-collars were found cached under 20 to 25 cm of soil.

TABLE 2. Comparison by age class[a] of proportions of skunks captured in March–July in east central North Dakota and west central Minnesota during 1979 through 1990[b] and Stutsman County, North Dakota in 1991 and 1992.

Age class	Comparison	Chi-square	df	*P*-value
1	1991 vs. 1992	16.13	1	0.0001
	1991 vs. 1979–1990	3.34	1	0.0677
	1992 vs. 1979–1990	28.63	1	0.0001
2	1991 vs. 1992	3.26	1	0.0710
	1991 vs. 1979–1990	0.35	1	0.5541
	1992 vs. 1979–1990	6.60	1	0.0102
3	1991 vs. 1992	6.05	1	0.0139
	1991 vs. 1979–1990	2.62	1	0.1056
	1992 vs. 1979–1990	7.62	1	0.0058

[a] Age class 1, <2-yr-old; age class 2, ≥2-yr-old and <3-yr-old; age class 3, ≥3-yr-old.
[b] Capture locations in 1979 through 1990 given in Greenwood and Sargeant (1994).

We documented only two interactions during the study between radio-collared skunks and persons on the study area. On 1 June 1991, an aggressive rabid skunk attacked a farmer during daytime; had we not euthanized the skunk, he would have shot it. On 18 June 1992, another farmer shot a skunk at twilight; he said it was "normal acting." Both skunks were positive for rabies.

Based on bite marks on live skunks and carcasses, we believe that aggressive interactions occurred both years between radio-collared skunks and other carnivores, including other skunks. In 1991, two (6%) of 31 skunks had 3 to 4 mm diameter punctures on their chest or abdomen; both animals were alive and appeared healthy when euthanized, in spite of the punctures. Neither was tested for rabies. Based on the 35 to 40 mm spacing between punctures, we believe bites were inflicted by a large carnivore, possibly coyote (*Canis latrans*), red fox (*Vulpes vulpes*), American badger (*Taxidea taxus*), raccoon (*Procyon lotor*), or domestic dog (*Canis familaris*); all these species were present on the study area.

TABLE 3. Number, location, condition, and rabies status of skunks found dead or euthanized during April to July 1992 in Stutsman County, North Dakota.

Location and condition of carcass or remains	Rabies status and number		
	Positive	Negative	Not tested
Found dead above ground			
Intact carcass	15	3	2[a]
Chewed collar only	0	0	1[b]
Found dead below ground			
Intact carcass	8	2	1[c]
Cached head only	3[d]	0	0
Euthanized above ground			
Clinical signs[e]	5	0	0
No visible clinical signs	5[f]	12	1
Lost or not radio-equipped	0	0	4
Total	36	17	9

[a] Brains were autolyzed; one skunk contained numerous porcupine (*Erethizon dorsatus*) quills in head and chest.
[b] Found only radio-collar with tooth impressions, consistent with those of a large canid.
[c] Broken bones were evidence vehicle collision caused lethal injury to animal.
[d] Found only severed head and neck with attached radio-collar cached under 20 to 25 cm of soil.
[e] Paralysis of hind limbs and heavy salivation.
[f] One skunk without apparent clinical signs was shot in farmyard.

TABLE 4. Size and location of bite marks and rabies status of 60 striped skunks found dead or euthanized in Stutsman County, North Dakota during April to July 1992.

Size and location of bite marks	Rabies status and number		
	Positive	Negative	Not tested
Large[a] punctures			
On body or head	7[b]	1	0
On detached radio-collar	0	0	1[c]
Small[d] punctures			
On limbs	2	0	1[e]
On limbs and head	5	2	0
On head	1	0	0
On attached radio-collar	1	0	0
Scars on muzzle	1	2	0
No bite marks or scars	19	12	1
Unknown	0	0	4
Total	36	17	7

[a] Punctures 3 to 4 mm diameter; spacing between punctures was about 35 to 40 mm, consistent with teeth of large canid.
[b] Includes three skunks whose heads were apparently severed by a large canid and cached.
[c] Radio-collar crushed severely, consistent with chewing by large canid.
[d] Punctures 0.5 to 1.0 mm diameter; when evident, spacing between punctures was about 10 to 15 mm, consistent with teeth of a skunk-sized animal.
[e] Contained numerous porcupine (*Erethizon dorsatum*) quills in head and chest.

In 1992, 17 (47%) of 36 rabid skunks and five (29%) of 17 healthy skunks had bite marks or scars (Table 4). Based on 0.5 to 1 mm diameter punctures with spacing of 10 to 15 mm, we believe small bites were inflicted by skunks or domestic cats (*Felis domesticus*). It appeared that most small bites were not self-inflicted, because 12 (86%) of 14 animals were bitten on the muzzle, head, or attached radio-collar. We did not determine if cached heads were scavenged or severed from live animals.

Two radio-collared skunks died in 1991, one (not tested for rabies) by vehicle collision and one (rabid) attributed to shooting. We detected no difference in 1991 in survival rates between males and females (chi-square = 2.72, 1 df, $P = 0.10$) or between age classes 1 and 2 (chi-square = 0.72, 1 df, $P = 0.40$). The estimated mean survival rate of 23 radio-collared skunks between 18 April and 20 June 1991 was 0.849 ± 0.070 (Table 5).

Thirty-nine radio-collared skunks died in 1992, 24 of rabies, nine by predation, one by vehicle collision, one by shooting, and four of unknown causes. We detected no difference in 1992 in survival rates between males and females (chi-square = 1.27, 1 df, $P = 0.26$); however, skunks in age class 1 survived at a lower rate than did skunks in age class 2 (chi-square = 8.10, 1 df, $P = 0.004$). The estimated mean survival rate of 56 radio-collared skunks between 31 March and 15 July 1992 was 0.17 ± 0.04 (Table 5).

Highest rate of mortality overall in 1992 tended to be from rabies (0.67) (Table 5). Rabies tended to have a slightly greater influence on mortality of males (0.80) than females (0.61), but we observed little dif-

TABLE 5. Causes of mortality, total days (Days) and number of mortalities (m) observed, estimated survival rates ($\hat{S}$)[a], mortality rates (Rate), and dates of last cause-specific mortality (Date) of striped skunks by Group (sex with age classes[b] combined, or age class with sexes combined) in Stutsman County, North Dakota during April to June 1991 and April to July 1992.

	Total observed				Cause of mortality								
					Rabies[c]			Predation[d]			Other		
Group	Days	m	$\hat{S}$	(SE)	Rate	m	Date	Rate	m	Date	Rate	m	Date
1991													
Males	63	0	1.000	(0.000)	0.000	0	—	0.000	0	—	0.000	0	—
Females	64	2	0.720	(0.120)	0.000	0	—	0.000	0	—	0.280	2	1 June
1[b]	63	1	0.833	(0.139)	0.000	0	—	0.000	0	—	0.167	1	15 May
2	64	0	1.000	(0.000)	0.000	0	—	0.000	0	—	0.000	0	—
Total[e]	64	2	0.849	(0.070)	0.000	0	—	0.000	0	—	0.151	2	1 June
1992													
Males	107	16	0.111	(0.060)	0.803	11	19 June	0.281	4	10 June	0.063	1	11 May
Females	103	23	0.205	(0.058)	0.606	13	11 July	0.241	5	19 June	0.225	5	18 June
1[b]	106	6	0.080	(0.054)	0.583	3	7 July	0.583	2	10 June	0.200	1	14 May
2	103	17	0.350	(0.078)	0.567	14	11 July	0.091	2	19 June	0.038	1	18 June
Total	107	39	0.173	(0.042)	0.671	24	11 July	0.290	9	19 June	0.174	6	18 June

[a] Kaplan-Meier survival estimates from staggered entry design (Pollock et al., 1989).
[b] Age class 1, <2-yr-old; age class 2, ≥2-yr-old.
[c] Includes some animals that tested positive for rabies.
[d] Columns do not sum to totals because ages were not estimated for all skunks.

ference in effects of rabies between age class 1 (0.58) and age class 2 (0.57). Another source of mortality, predation by large carnivores, tended to have similar influence on mortality of males (0.28) and females (0.24). Skunks in age class 1, however, tended to suffer greater mortality from predation by large carnivores (0.58) than did older skunks (0.09). Seven of the nine skunks whose deaths we attributed to predation were rabid.

We observed considerable variation in mean nightly rates of travel of skunks by half-month period, with no consistent trends. We detected no differences in mean rates of travel due to main effects of sex, rabies condition, or their interaction ($P \geq 0.10$). The mean rate of travel in a night between 19 April and 25 June for all skunks was 232 ± 14 m/hr.

Variation in rates of travel of both healthy and rabid skunks in 1992 was low (2 to 8%) due to differences between animals. However, rates of travel were nearly twice as variable between animals on different nights for rabid skunks (females, 23%; males, 33%) as for healthy skunks (females, 10%; males, 16%). Conversely, variation in rates of travel due to differences between locations within nights was less for rabid skunks (females, 75%; males, 65%) than for healthy skunks (females, 85%; males, 76%).

We detected considerable variation in mean nightly distance traveled by skunks by half-month period, with no consistent trend. We detected no differences in mean distances traveled in a night by skunks in 1992, due to main effects or their interaction ($P \geq 0.23$). Mean distance traveled in a night during 19 April to 25 June was 2,047 ± 141 m.

We detected no differences in half-month home range estimates of skunks in 1992 due to main effects or their interaction ($P \geq 0.23$). However, there was a tendency for half-month home range sizes of all skunks to differ by half-month period ($F = 2.31$; df = 4,75; $P = 0.07$). Mean estimates of home range size tended to in-

TABLE 6. Least-squares means of minimum rate of travel in a night (Rate), minimum distance traveled in a night (Distance), and Home range of radio-collared striped skunks with rabies in the 14 days before the clinical period of rabies (pre-clinical) and during the 14-day clinical period, Stutsman County, North Dakota from April to July 1992.

Sex	Stage	Rate (m/hr)		Distance (m)		Home range (km^2)	
		Number	Mean ± SE	Number	Mean ± SE	Number	Mean ± SE
Male	Pre-clinical	8	313 ± 72	8	2,453 ± 419	8	2.8 ± 0.4
	Clinical	8	187 ± 72	8	1,566 ± 419	8	1.8 ± 0.4
Female	Pre-clinical	10	282 ± 64	10	2,183 ± 375	9	1.2 ± 0.4
	Clinical	10	160 ± 64	10	1,428 ± 375	9	1.8 ± 0.4

crease between late April (1.1 ± 0.5 km^2) and late May (2.1 ± 0.5 km^2). The overall mean home range size during 19 April to 25 June was 1.6 ± 0.4 km^2.

Among skunks with rabies in 1992, mean rate of travel tended to decrease between the pre-clinical period (298 ± 48 m/hr) and clinical period (174 ± 48 m/hr) (F = 3.32; df = 1,16; P = 0.09) (Table 6). We detected no difference in mean rates of travel between males and females (F = 0.18; df = 1,16; P = 0.68), and no interaction between sex and period (F = ≤0.01; df = 1,16; P = 0.98).

The mean distance traveled in a night by skunks with rabies tended to be greater during the pre-clinical period (2,318 ± 281 m) than during the clinical period (1,497 ± 281 m) (F = 4.26; df = 1,16; P = 0.06) (Table 6). We detected no difference between males and females in mean distances traveled (F = 0.20; df = 1,16; P = 0.66) and no interaction between sex and period (F = 0.03; df = 1,16; P = 0.87).

The mean home range size of skunks with rabies varied by sex between pre-clinical and clinical periods (F = 4.67; df = 1,15; P = 0.05) (Table 6). We detected no difference in the home range size of males between the pre-clinical and clinical period (P = 0.10). During the pre-clinical period, home range size of males was greater than that of females (P = 0.01), but during the clinical period we detected no difference between home range sizes of males and females (P = 0.94). We detected no difference in home range size of females between pre-clinical and clinical periods (P = 0.22).

The pattern of deaths of rabid skunks tended to be more spatially clumped within the radio-collared population than if deaths were entirely random (P = 0.08). Much of the influence on spatial clumping was from deaths of the first nine skunks between 2 April and 7 May (Table 7); all nine were clustered within 3.2 km of the location of the first death (Fig. 1). Three of the nine were represented only by heads cached within 1.6 km of each other. After 7 May, deaths from rabies tended to be more generally distributed throughout the population.

We did not detect a correlation between activity centers of skunks that died of rabies and dates of death (r = −0.02, P = 0.66). Although skunks that died of rabies between 2 April and 7 May tended to be located relatively close together in space and time, the relationship was less evident after 7 May.

We used information on 49 radio-collared skunks to evaluate use of feeding sites in 1992. Ten skunks were never detected at a feeding site. Thirty-nine animals visited feeding sites on 170 (6%) of 2,946 occasions during night-tracking when located away from daytime retreats. Nine of the 39 animals were detected at a site only once and none was detected at more than one feeding site in an individual night. Only one skunk was detected at more than one feeding site during 1992; it was a 4-year-old rabid male that visited

TABLE 7. Number of radio-collared striped skunks observed during 1992 in Stutsman County, North Dakota, cumulative number found dead from rabies, date on which at least one skunk was found dead, and likelihood (percent) of finding a more clumped distribution than we observed.

Date	Number of skunks		Likelihood (percent) of a more clumped distribution
	Observed	Dead (cumulative)	
2 April	15	1	NE[a]
13 April	30	2	9
16 April	30	4	1
27 April	30	7	8
2 May	38	8	20
7 May	38	9	26
11 May	38	11	46
19 May	41	12	55
21 May	41	13	30
23 May	41	14	30
27 May	41	15	59
31 May	43	16	81
3 June	43	17	92
5 June	43	19	89
9 June	43	20	83
10 June	43	23	37
12 June	43	24	64
18 June	43	25	58
19 June	43	27	50
23 June	44	28	33
29 June	48	29	23
3 July	48	31	28
7 July	48	32	19

[a] NE, not estimated where $n = 1$.

two adjacent sites on different nights. On 10 different occasions, more than two radio-collared skunks were detected at the same feeding site within 30 min of each other. Use of feeding sites varied between males and females depending on rabies condition ($F = 9.16$; df = 1,45; $P = 0.004$). Females with rabies were located at feeding sites more than twice as often (8%) as healthy females (3%) ($P = 0.03$). Conversely, males with rabies were located at feeding sites only half as often (4%) as healthy males (10%) ($P = 0.04$).

DISCUSSION

Rabies is enzootic in striped skunks in North Dakota, where in some years, skunks may account for all of the submitted rabies-positive cases (Charlton et al., 1991). In 1992, however, the epizootic we observed in Stutsman County likely would have been undetected without our study. None of the residents of our study area was aware of the rabies epizootic until we informed them of it in mid-May. Few skunks that died of rabies during March through July 1992 were visible to the public; nearly one-third of the carcasses or remains were below ground (Table 3). Most carcasses above ground were concealed in vegetation and, had we not retrieved them, would have decomposed within a few days.

In 1992, 115 cases of rabies in striped skunks were reported in North Dakota (Krebs et al., 1993). Of 40 cases reported from Stutsman County, 36 were from our study. Our estimate was a minimum; four skunks died or were released before we decided to test for rabies, two decomposed before we recovered their remains, and two others were not recovered. One of the decomposed skunks contained numerous porcupine (*Erethizon dorsatum*) quills; thus it may have been rabid (MacInnes, 1987). Without our sample, cases of rabies in 1992 would have been underestimated by a minimum of 31% in the state and by 90% in the county. Considering the above factors and relatively small area from which we obtained animals, the magnitude of underestimating of rabies deaths in striped skunks probably was greater than that. Overestimation may be more common, however, because high proportions of skunks submitted for necropsy are rabid, thus inflating estimates of proportions of rabid animals in populations (Gunson et al., 1978).

We cannot explain the etiology of lymphocytic meningitis in the four skunks that were negative for rabies and canine distemper. Two were found dead in May and the two others were euthanized in July and appeared to be healthy. None of the four had evidence of fighting or clinical signs of rabies. Based on these observations, we believe another virus or other unknown agent may have affected these animals.

In 1992, only 22% of skunks we captured were age class 1 (Table 1). In 1991, however, 66% of the skunks were age class 1. Greenwood and Sargeant (1994), likewise, found a high proportion (74%) of age class 1 animals among skunks examined from eastern North Dakota and western Minnesota between 1979 and 1990. First year animals usually compose about 45 to 50% of populations of healthy striped skunks (Casey and Webster, 1975; Schowalter and Gunson, 1982). Based on the disparity in age structure in 1992, we believe disease or other notable factor affected the first year animals, as suggested by Fuller and Kuehn (1985).

We suspect that rabies in 1991 may have affected productivity of females in the vicinity of our study area and consequently, reduced numbers of juveniles available to disperse to our area. In 1991, we confirmed rabies in one radio-collared skunk on the extreme north edge of our study area and had an unconfirmed report of another rabid skunk approximately 3.2 km northwest of there.

That rabies may have affected productivity was supported by our finding that only 72% of females we observed in 1992 were pregnant or parous. Pregnancy rates usually are considerably higher (Bjorge et al., 1981; Schowalter and Gunson, 1982). Greenwood and Sargeant (1994) reported a pregnancy rate of 95% in striped skunks from eastern North Dakota and western Minnesota during 1979 through 1991.

Although rabies is not known to affect implantation rate or embryo mortality, there are several other ways in which rabies may affect productivity. At northern latitudes, striped skunks breed in February and March (Greenwood and Sargeant, 1994), when they frequently occupy communal dens (Gunson and Bjorge, 1979). Although males seldom den together, individual males commonly den concurrently with several females (Houseknecht and Tester, 1978). Communal dens provide a focus for rabies transmission (Rosatte, 1984). Aggressive behavior that is characteristic of skunks with rabies (Charlton et al., 1991) might affect breeding success (Verts, 1967).

The influence of rabies on productivity likely would be additive to other factors that affect skunk populations. Adult skunks and American badgers prey on young skunks in natal dens (Sargeant et al., 1982) and juvenile skunks at northern latitudes may suffer high mortality due to stress and starvation during winter (Schowalter and Gunson, 1982; Fuller and Kuehn, 1985). Based on our findings, we believe that juvenile skunks also are more vulnerable to disease, in this instance rabies, and to predation, than are older skunks (Table 5). At northern latitudes, juvenile skunks commonly disperse from natal areas in fall (Bjorge et al., 1981) when incidence of rabies in skunk populations is high (Hayles and Dryden, 1970), compounding risks to juveniles.

We could not distinguish effects of disease from predation. Seven of the nine skunks whose deaths we attributed to predation were rabid. They may have been predisposed to predation because of changes in behavior or could have been scavenged by a predator after death from rabies. Regardless of the proximate cause of death, however, the ultimate cause of death would have been rabies.

We observed relatively consistent patterns of variation in rates of travel within groups of healthy and rabid skunks. Healthy animals tended to follow a nightly pattern of rapid movement, punctuated periodically with periods of slow movement, possibly while animals foraged. Among rabid skunks, however, rates of travel were erratic within nights, especially during the clinical period when we observed prolonged periods of inactivity on some nights. Some rabid skunks became virtually immobile 2 to 3 days before death. The five skunks we euthanized in the late clinical stage of rabies moved less than 100 m in their final 2 to 3 days.

Our estimates for healthy skunks of average distance traveled in a night and of home range size were slightly lower than reported by Greenwood et al. (1985), who monitored striped skunks in east-central North Dakota during 1977 and 1978. Those authors reported that females traveled 2,650 and males 3,300 m/night during late April. They estimated home range sizes during the same period of 2.4 km^2 for females and 3.1 km^2 for males.

We detected no evidence of heightened activity by males or females during the 14-day period before death, which we attributed to the clinical stage of rabies. Rates of travel and distances traveled in a night decreased markedly during the clinical period for both sexes, as did home range size of males. Storm and Verts (1966) concluded that movements of a radio-collared female striped skunk with rabies during the week before her death were not notably different from other female skunks they monitored at that time of year. Andral et al. (1982) likewise detected no change in home range of three radio-collared red foxes with rabies between the pre-clinical and clinical period. However, they reported a change in use of habitat and in diel activity patterns of foxes during the clinical period of rabies. Our sampling scheme was not designed to monitor daytime activity. However, the first radio-collared skunk we found in 1992 with rabies was observed staggering along a roadside at about 1300 on 10 April, 3 days before we found it dead of rabies only 60 m away. Healthy skunks seldom ventured far from their retreats during daytime in April and May in North Dakota (Greenwood et al., 1985). Parker (1962) suggested that skunks observed to be active during daytime are likely to be rabid.

Among skunks we monitored in 1992, rabies appeared to spread first between animals in the center of the radio-collared population. After the first eight or nine animals died, however, there was little consistency to the pattern of deaths of the animals that remained. We do not know when individual animals became infected. Based on dates of death of the skunks that we first found dead of rabies, infection easily could have occurred in winter dens. The incubation period of rabies in striped skunks may vary from 18 to 41 days (Gough and Niemeyer, 1975), but can be considerably longer (Charlton et al., 1991), thus some skunks we monitored may have been infected for several months before we captured them.

Our feeding sites provided a continuous source of food, but we believe they probably did not influence movements or interspecific contact of skunks more than farm middens where skunks are known to forage (R. J. Greenwood, unpubl.). Although Seidensticker et al. (1988) suggested that radio-collared raccoons, some of which were rabid, moved their dens closer to sites where food was provided, we had no direct evidence that our food manipulations affected rates of travel, distances traveled, or home range sizes of skunks. We cannot explain differences in visitation rates to feeding sites by male and female skunks in relation to rabies status.

Rabies virus typically is transmitted in saliva by biting (Charlton et al., 1991) and we had strong evidence of biting among skunks, as well as among skunks and other carnivores, possibly including coyotes, red foxes, American badgers, raccoons, dogs, and cats. We also detected three cached heads of skunks, which is evidence that carcasses had been eaten. Transmission by eating tissue of a rabid animal is possible (Ramsden and Johnston, 1975). In spite of these interspecific contacts, however, we are not aware of spillover into other species, wild or domestic, during the rabies epizootic we observed. Other than striped skunks, we know of only one animal diagnosed with rabies in the locality of our study area in 1992. That was a red fox about 16 km southwest of our study area. Thus, although the behavior and timing of movements of striped skunks at northern latitudes are conducive to spread of rabies (Sargeant et al., 1982), this epizootic apparently was confined to skunks, and probably would have been undetected without our monitoring.

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