MASTER

MOVEMENTS, ACTIVITY PATTERNS AND DENNING
HABITS OF STRIPED SKUNKS (*Mephitis mephitis*)
AND THE EXPOSURE POTENTIAL FOR DISEASE

A THESIS
SUBMITTED TO THE FACULTY OF THE GRADUATE SCHOOL
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ABSTRACT

The movements, activity patterns and denning habits of striped skunks (Mephitis mephitis) were studied between March 1968 and November 1969 with the aid of an automatic radio-tracking system.

There was marked individual and seasonal variation in home range size. The data suggested that females had slightly larger ranges than males but this might have resulted from seasonal shifts of activity centers. Ranges of both males and females were linear and certain areas were used more intensively than other areas. Skunks preferentially selected upland open habitats. Both males and females avoided lowland open areas and males avoided upland wooded habitat as well.

The incidence of daytime activity of skunks was higher than that reported by previous workers. Levels of activity during summer months indicated that, up to a point, skunks were able to meet nutritional requirements by increased feeding activity during nighttime hours. When food resources were scarce or when nutritional requirements were high, daytime feeding became necessary. Cosine analysis demonstrated that skunks have true circadian activity rhythms.

Locations of thirty-six skunks were field checked a total of 1627 times. Physical characteristics of 206 dens and 183 aboveground rest sites were recorded. There was a general shift from underground, upland dens in winter to aboveground, lowland dens in summer. Significant intraspecific contact

occurred through concurrent and sequential use of underground dens and hollow logs. Den sharing occurred only between the third week of October and the first week of April. Only one aboveground rest site was used by more than one skunk. Both males and females changed den locations frequently. The average straight line distance between successive den sites was .30 mile. It was concluded from this study that movements, activity patterns and denning habits of skunks result in a high exposure potential for disease transmission.

INTRODUCTION

Since the time of the early Greeks and Romans there has been an appreciation of the role of lower animals in the health and well-being of man. Hippocrates, Marcus Terrestius Varro, and Nicandros of Colophon wrote of real and fancied associations between the diseases of man and lower animals (Schwabe, 1969). Fracastro in his book, "Contagion" (ca. 1546), gave a vivid description of the transmission of rabies from dogs to humans (Meyer, 1931). Jenner, in 1796, discovered that a disease of cows, cowpox, was related to a similar malady in man and Lenckart in the middle of the 19th century demonstrated the significance of animal life cycles in human helminth infections (Meyer, 1931).

The concept of animals as reservoirs of disease came later, however, with much of the impetus for research stimulated by Elton's (1931) classic paper. Since then, all major phyla of animals have been implicated in the maintenance or spread of diseases which directly infect man or which assume economic importance by causing loss of domestic animals or desirable wildlife species. Swain (1961) listed 9 bacterial, 4 rickettsial and 32 viral diseases transmitted from wild animals to man.

Vertebrates are perhaps the most important animals in this respect. Karstad (1961) speculated on the role of reptiles as reservoirs of eastern equine encephalitis virus and birds, especially migratory species, are known to be important in the spread of several disease organisms including eastern equine, western equine and St. Louis encephalitis viruses (Hoogstrall,

1961; Stamm, 1963). Applegate (1968) reported that populations of house sparrows (Passer domesticus) can maintain latent experimental parasitemias of avian malaria (Plasmodium spp.) for considerable periods of time. Deane (1964), Kartman (1960), and Sulkin (1962) demonstrated the role of certain small mammals as reservoirs of trypanosoma, plague, and rabies, respectively.

Striped skunks are regarded as likely reservoirs of at least three important zoonoses; rabies, leptospirosis and tularemia, and in addition, are known to be susceptible to canine distemper, Q fever, listeriosis, pulmonary aspergillosis, murine typhus, and chagas disease (Verts, 1967). Thus the potential role of the striped skunk in the ecology of these and other diseases is of prime importance.

Several authors (e.g. McKeever et al., 1958; Roth et al., 1963; Ferris and Andrews, 1966) have given the incidences of some important zoonoses in striped skunk populations but only Verts (1967) has attempted to relate the overall biology of the species to a particular disease complex (rabies). Verts, however, had few or no data on certain biological characteristics of striped skunks which potentially have great bearing on the role of this species in the ecology of rabies and other diseases as well. For example, most of Verts' movement and activity data came from juvenile animals that were radio-tracked only for brief periods and he did not report on the amount of intraspecific contact and the resulting exposure potential for disease.

Recently, Pavlovsky (1966) and others have developed the concept of natural nidality of disease and have stressed the need for synecological investigations of disease foci. The concept of natural nidality can be best thought of in terms of mathematical set theory in which the disease complex represents the set and the associated chemical, physiological, behavioral and biogeographical characteristics of the causative organism, host, vector, vehicles and environment, represent the subsets. If the set (disease complex) is to be understood the characteristics and interrelationships of the subsets must be known in detail. For most important zoonoses much is known about the biology and natural history of the causative organism and its spread from the wildlife reservoir to man. Often, however, very little is known of the behavior of associated reservoir species or of the transmission from host to host.

I hypothesize that interspecific and intraspecific contact in striped skunk populations is related to behavioral characteristics such as home range size and location, habitat preference, activity patterns, and denning habits. Schwabe (1969, p. 70) terms these factors "interactions of a population with its environment" and hence "fit subjects for the student of medical ecology". The overall objective of this study was to relate the above behavioral patterns to direct and indirect contact and the resulting exposure potential for disease.

STUDY AREA

This investigation was conducted on the Cedar Creek Natural History Area (CCNHA) 30 miles N of Minneapolis, Minnesota. The topography is flat to gently rolling with sandy upland areas interspersed with sedge (Carex spp.) meadows, white cedar (Thuja occidentalis) and alder (Alnus rugosa) swamps, cattail (Typha latifolia) marshes, cultivated and abandoned cropland, two small lakes and a creek. Bray et al. (1959) classified the upland cover as mixed conifer-angiosperm forest, deciduous-angiosperm forest and tall-grass prairie. The predominant upland trees are oaks (Quercus ellipsoidalis, Q. macrocarpa, Q. alba, Q. rubra) and pines (Pinus resinosa, P. strobus) with scattered basswood (Tilia americana) and sugar maple (Acer saccharum) with a dense hazel (Corylus cornuta) understory. White cedar, tamarack (Larix laricina) and alder dominate the lowland forest with such associated species as red osier (Cornus stolonifera), willow (Salix spp.), white birch (Betula papyrifera) and aspen (Populus tremuloides). The principal cultivated crops are corn (Zea mays), soybeans (Lens esculenta), Alfalfa (Medicago sativa), and rye (Secale cereale). Rongstad and Tester (1969) subjectively categorized the 16 square miles containing and surrounding CCNHA as 64 percent upland (23 percent woods, 41 percent fields); 32 percent lowland (18 percent marsh, 14 percent wooded swamp); and 4 percent open water.

The upland soil is Zimmerman sand composed of pure greyish quartz with 40-60 percent very fine particles and almost no

pebbles or coarse fragments. The soil is a typical podzol with a deeper than usual A horizon extending to depths of 3-5 feet. Lowland peat soils are of two types: 1) spongy forest peats with incorporated Sphagnum moss and 2) fibrous sedge peat which has developed under sedge vegetation around the bog lakes (Pierce, 1954).

The normal length of the frostless season is mid-May to the end of September but in low areas no month can be presumed to be frost-free. The normal period of snow cover is about 30 November to 15 March. Mean annual precipitation is 26.56 inches (Pierce, 1954).

During this study (October 1967 to November 1969) temperatures ranged from -33° to 95°F with an average monthly maximum and minimum of 79°F (July and August) and -4°F (January) respectively. Weather data were recorded at the U.S. Weather Bureau Station at CCNHA.

MATERIALS AND METHODS

Study animals were captured, anesthetized with ether, weighed, sexed and aged. Blood, urine, saliva, and fecal samples were taken for other investigations. Three capture methods were employed; live-trapping in National style box traps, excavation of dens, and live traps set in enclosures surrounding active den sites.

During 1967 and 1968 live traps were set at likely locations (primarily along a network of dirt roads within the study area)

and were operated at irregular intervals. In 1969 live traps were again set at likely capture locations but were operated for one week each month. Animals were classified as juveniles or adults on the basis of weight, tooth wear, and, in the case of females, the length, diameter, and color of teats (Verts, 1967).

Skunks were tagged with radio transmitter collars weighing about 75 gm (Cochran and Lord, 1963; Mech et al., 1965) and were released where captured. Each transmitter operated on a different frequency. Animals were recaptured at approximately 5-month intervals for the replacement of transmitter batteries. An automatic radio tracking system (Cochran et al., 1965) recorded on microfilm the activity status and approximate locations of all skunks in terms of angular coordinates relative to each of two towers. These towers, located 0.5 miles apart, support receiving antennae that rotate at 1-1/3 rpm.

The film was read on a microfilm reader to the nearest degree. Locations or "fixes" of moving animals were sampled at 10 minute intervals for 10 days each month resulting in approximately 700 to 1000 locations per month for each animal. During skunks' daytime rest periods hourly checks of the microfilm were made to determine if movement had occurred and, if not, all fixes for that period were lumped together. For purposes of determining certain denning parameters, fixes were also obtained each day at 1100, 1200, and 1300 hours C.S.T. If the bearings of all three locations were within

plus or minus 1° the skunk was assumed to be in a den or daytime rest site (major rest period). Sex, age, transmitting periods, and total number of days tracked for each skunk are given in Table 1.

Since the tracking system depends on triangulation to locate an animal, a misreading of the film record by 1° produces different distance errors in various parts of the coordinate system. For example, in certain areas near either of the towers, a 1° error amounts to only 10 ft whereas two miles from the tower it might mean 800 ft. Near an imaginary line connecting the two towers and extending beyond them, called the base line, a 1° error can be as much as $1/4$ mile. In addition to the 1° film reading error, there is a possible error of as much as 0.5° because an animal is rarely found where an exact intersect falls (Heezen and Tester, 1967). Thus, in some areas, locations 200 ft apart appear as the same point to the system. Sargeant et al. (1965) classified the study area into zones within which an error of 1° would amount to certain maximum distances; e.g. their 200 ft zone is the area in which a 1° misreading gives an error of not more than 200 ft. They also found that actual errors were seldom as large as this maximum distance, and that they averaged much less. Some skunks monitored in this study were often in areas of poor accuracy and their movements are not included in the detailed analyses below.

Table 1. Sex, age, transmitting periods and number of days tracked for each study animal.

Number	Sex	Age	Transmitting Period(s)	Days Tracked
1201	Male	Ad	5 Oct 67 - 7 May 69	579
1202	Male	Ad	5 Oct 67 - Died in winter den	
1203	Male	Juv	8 Oct 67 - 23 May 68	228
1204	Female	Ad	13 Oct 67 - 29 Feb 68 and 19 Mar 68 - 19 June 68	231
1205	Female	Juv	13 Oct 67 - 13 June 68	244
1206	Female	Juv	21 Oct 67 - Died in winter den	
1207	Male	Ad	21 Oct 67 - 5 Aug 68	269
1208	Male	Ad	23 Oct 67 - 16 April 68	176
1209	Male	Juv	25 Oct 67 - 17 April 68	175
1211	Female	Ad	18 Mar 68 - 20 May 68	63
1212	Male	Ad	27 Mar 68 - 18 Aug 68 and 30 April 69 - 14 Nov 69	342
1213	Female	Ad	27 Mar 68 - 25 Aug 69	151
1214	Female	Ad	27 Mar 68 - 17 June 68	82
1215	Male	Ad	28 Mar 68 - 5 Nov 68	222
1217	Male	Ad	2 April 68 - 25 Sept 69	541
1232	Female	Ad	26 June 68 - 3 April 69	281
1233	Female	Ad	27 June 68 - 22 April 69	299
1235	Male	Juv	27 June 68 - Died in winter den	

Table 1. Continued.

Number	Sex	Age	Transmitting Period(s)	Days Tracked
1236	Male	Ad	14 July 68 - 14 Feb 69	215
1238	Male	Ad	17 July 68 - 22 Oct 68	97
1241	Male	Ad	28 July 68 - Died in winter den	
1242	Female	Ad	28 April 69 - 30 Nov 69	116
1244	Female	Ad	22 Oct 68 - 8 April 69	168
1245	Male	Ad	22 Oct 68 - 9 April 69	169
1246	Female	Ad	23 Oct 68 - 18 Dec 68	55
1247	Female	Juv	24 Oct 68 - Slipped collar in winter den	
1248	Female	Juv	30 Oct 68 - Died in winter den	
1249	Male	Ad	4 Nov 68 - 19 May 69	196
1250	Female	Juv	4 Nov 68 - 28 April 69	175
1251	Female	Ad	22 Mar 69 - 29 Mar 69	7
1253	Male	Ad	8 April 69 - 29 April 69	21
1255	Male	Ad	3 May 69 - 3 July 69	61
1256	Male	Ad	3 May 69 - 22 Sept 69	142
1258	Male	Ad	29 June 69 - 30 Nov 69	154
1264	Female	Ad	21 July 69 - 16 Oct 69	87
1269	Female	Juv	19 Aug 69 - 30 Nov 69	103
1271	Female	Juv	19 Aug 69 - 9 Sept 69	21

Table 1. Continued

Number	Sex	Age	Transmitting Period(s)	Days Tracked
1272	Male	Ad	20 Aug 69 - 29 Aug 69	9
1273	Male	Juv	23 Aug 69 - 10 Sept 69	18
1275	Male	Juv	18 Sept 69 - 30 Nov 69	73

Additional data on movement and denning habits were obtained by field checking radio-marked skunks with a portable direction finding receiver (Cochran and Lord, 1963). Between 1 November 1967 and 7 March 1968 and between 15 November 1968 and 7 April 1969 each radio-tagged skunk was located at least three times per week. During the remainder of the study period I attempted to locate three randomly selected individuals each day Monday through Friday. Each den and aboveground rest site was marked with an identifying tag and was classified as to habitat type, distance to the nearest edge, adjacent habitat type and the number and size of openings.

There was no indication that these field checks disturbed skunks in underground dens, hollow logs or den trees. However, animals in aboveground rest sites often moved away when approached by the observer.

Radio telemetry data were analyzed on a Control Data 6600 computer with an extensive series of programs written especially for the tracking system at CCNHA. One of these programs relates animal movements to previously coded habitat types. For this program CCNHA was divided into 1.6 acre squares (0.0025 square mile) and each square was categorized into one of 54 habitat types. In view of the accuracy limitations discussed above and the objectives of this study, these habitat classifications were lumped into four broad categories: lowland open (e.g. marsh, bog), lowland wooded (e.g. cedar

and alder swamps), upland fields and upland wooded (e.g. oak forests and mixed upland woods).

Other programs measure home ranges and intensity of use of each part of the home range by again dividing CCNHA into 1.6 acre squares and determining the location of squares containing fixes and the number of fixes in each square. A boundary was put on the home range by searching alternately along the horizontal and vertical axes from squares containing fixes. Squares with fixes that were separated along either axis by not more than two vacant squares were considered to be within the boundary. Home range size was determined by summing the squares within the boundary. The limitations of this method have been discussed by Rongstad and Tester (1969).

RESULTS

Home range size varied markedly between individuals and seasonally, within individuals (Table 2). I did not monitor a sufficient number of animals for more than two tracking periods (Table 2) to form definite conclusions on seasonal variations of range size; however, some trends are evident. Males tended to have larger home ranges during Periods 1 (March and April) and 2 (May and June) than during Periods 3 (July, August and September) and 4 (October and November). Although no quantitative data were obtained on abundance of food items, my impression was that grasshoppers, which examination of scats showed to be a major dietary component, were relatively scarce during Periods 1 and 2.

Table 2. Home range (square miles) of skunks for each radio-tracking period.

Skunk	Tracking Period								
	1967	1968				1969			
	4	1	2	3	4	1	2	3	4
1201 Male	0.32	0.84	0.90	0.75	0.26	0.66			
1203 Male	0.52	0.70	0.22						
1207 Male	0.23	0.79	0.66	0.58					
1209 Male	0.45								
1217 Male		0.56	0.62	0.62	0.51	0.55	0.50	0.70	
1235 Male				0.74	0.24				
1241 Male					0.15				
1255 Male							0.46		
1256 Male							0.22		
1273 Male								0.24	
1275 Male									0.88
1204 Female	0.11	0.42	0.57						
1211 Female		0.80	0.37						
1232 Female				1.12	0.32				
1233 Female				1.04	0.40				
1242 Female							0.40	1.40	0.59
1250 Female						0.43			
1269 Female								0.34	

Period 3 ranges of three adult females (1232, 1233, 1242) were larger than those for the same animals during Period 4 and larger than those of any male for that period. In the first half of Period 3 females are lactating and require a considerable amount of food. In addition, two of three adult females shifted their range after breakup of the family group in the last half of Period 3. Heavy use of two different areas during the same tracking period tends to increase the size of the apparent home range. Both males and females showed a decrease in home range size during Period 4. At this time skunks have reached their maximum weight and have begun to prepare and use winter dormancy dens. Activity radii (Hayne, 1949) for each tracking period support the above generalizations. Mean radii for males declined almost linearly from Period 1 through Period 4. Females evidenced the longest activity radii during Period 3 (Figure 1).

A composite home range size was computed for the total tracking period for each skunk located more than an arbitrary minimum of 850 times. Home range size was strongly correlated ($r = .80$) with the number of days the animals were radio-tracked (Table 3) and for this reason it was not felt advisable to calculate an overall average range size for males or females. Range sizes of 1.93 and 1.37 square miles per 100 days tracked for females and males, respectively, suggest that ranges of females are larger than those of males.

Figure 1. Mean length of activity radii (Hayne, 1949) for male (A) and female (B) striped skunks. Vertical lines represent the range of values. Numbers in parentheses indicate sample sizes.

Table 3. Size of apparent home range as related to the number of days radio-tracked.

Animal	Days Tracked	Home Range Size (sq. miles)
1201 Male	164	1.73
1203 Male	65	1.01
1207 Male	82	1.25
1217 Male	152	1.83
1235 Male	53	0.86
1275 Male	35	0.88
1204 Female	85	0.75
1211 Female	32	0.97
1232 Female	60	1.39
1233 Female	60	1.24
1242 Female	85	1.71
1250 Female	15	0.43

Frequent den checks indicated, even before analysis of movement patterns, that some skunks were much more mobile than others. For example, adult male 1203 denned repeatedly in a small alder-sedge swamp in June 1968 while at the same time adult male 1201 changed dens frequently, with successive locations often more than a mile from the previous den site.

Temporal development of apparent home range size was investigated by summing daily ranges of four selected animals and then calculating the cumulative increase in total range (Figure 2). Two skunks evidenced a tendency for no further increase in range size after 84 and 146 days of tracking. Ranges of the other two individuals did not appear to reach their ultimate size at 51 and 54 days. These data and the strong correlation between range size and the number of days tracked suggest that striped skunks either do not have definite home range limits or that periodic range shifts obscure limits that do exist.

Length of each composite home range was determined by drawing a straight line (L) between the most distant plotted fixes. Range width was computed as the sum of the perpendicular distance to L from the most distant point on either side of L. Average range length and width and the average index of linearity (length/width) were remarkably similar for males and females (Table 4).

Intensity of use for each 1.6 acre portion of each composite home range was computed as:

$$\frac{N_i}{N} \times 100 \quad \text{where } N_i \text{ represents}$$

Figure 2. Cumulative increase in home range of striped
skunks.

DAYS RADIO - TRACKED

Table 4. Ratio of range length to width for male and female skunks.

Skunk	Range (Miles)		Length/Width
	Length	Width	
1201 Male	2.36	1.56	1.51
1203 Male	1.54	1.16	1.33
1207 Male	1.80	1.50	1.20
1217 Male	2.34	1.60	1.46
1235 Male	1.48	0.92	1.61
1275 Male	1.66	0.94	1.76
$\bar{X}$ males	1.86	1.28	1.48
1204 Female	1.56	0.92	1.70
1211 Female	1.62	1.52	1.06
1232 Female	2.14	1.76	1.22
1233 Female	2.06	1.42	1.45
1242 Female	2.20	1.38	1.59
1250 Female	1.00	0.60	1.67
$\bar{X}$ females	1.76	1.27	1.45
$\bar{X}$ total	1.82	1.27	1.46

the number of fixes occurring in grid square i and N equals the total number of fixes in the home range. The results (Figures 3 and 4) show that range utilization is not uniform; some areas receive much more use than others. For all three females tracked during lactation (1204, 1211 and 1242) the area of highest use lay very close to the location of the natal den.

Two or more disjunct areas of high use within the same range (e.g. 1201, 1203 Figure 3; 1232, 1233 Figure 4) could result from denning and feeding areas separated by habitat that was not particularly conducive to either activity or could result from definite range shifts.

Patterns of habitat usage were investigated by determining the percentage of total fixes in each vegetation category (V_{t1}) and the percentage of the same types (V_{t2}) available within the boundary of the range for each ten-day sampling period. A positive value for $V_{t1} - V_{t2}$ indicates a selection for vegetation type t . Conversely, a negative value for the same expression indicates selection against that habitat type.

There was great variation between individuals and no seasonal trends were evident (Figures 5-8). Total habitat preferences of males and females are summarized in Table 5.

Data were analyzed for seasonal patterns of onset and cessation of activity, temporal levels, and amount of daytime activity by partitioning the non-winter denning portion of the year into time periods related to parturition, lactation and

Figure 3. Intensity of use of the home range by male striped skunks.

1201

1203

- 3.1 - > Percent of total fixes
- 2.1 - 3.0 Percent of total fixes
- 1.1 - 2.0 Percent of total fixes
- .6 - 1.0 Percent of total fixes

1207

1217

ONE MILE

1235

1275

Figure 4. Intensity of use of the home range by female striped skunks.

1204

1211

- 3.1 - > Percent of total fixes
- 2.1 - 3.0 Percent of total fixes
- 1.1 - 2.0 Percent of total fixes
- .6 - 1.0 Percent of total fixes

1232

1233

ONE MILE

1242

Figure 5. Skunk utilization of available upland open habitat. A positive value for $V_{t1} - V_{t2}$ indicates a selection for that habitat type.

Figure 6. Skunk utilization of available upland wooded habitat. A positive value for $V_{t1} - V_{t2}$ indicates a selection for that habitat type.

Figure 7. Skunk utilization of available lowland open
habitat. A positive value for $V_{t1} - V_{t2}$
indicates a selection for that habitat type.

Figure 8. Skunk utilization of available lowland wooded habitat. A positive value for $V_{t1} - V_{t2}$ indicates a selection for that habitat type.

Table 5. Habitat preferences of striped skunks for all ten-day tracking periods. The values represent only a selection for or an avoidance of a particular habitat type and do not indicate the strengths of the phenomena.

	Selection (+)/avoidance (-)			
	Upland Open	Upland Wooded	Habitat Type Lowland Open	Lowland Open
Males	29/32	21/42*	12/48**	26/33
Females	17/11	13/16	2/24**	11/17
Total	46/43	34/58	14/72**	35/50

*Sig. < .05 Sign Test

**Sig. < .01 Sign Test

dispersal of the young. Data for each radio-tracked skunk during each time period were compressed into a single 24 hour "day" and the percent of radio fixes indicating activity was computed for each of 144 ten minute intervals throughout the day. Within sex, data were similar during equivalent periods for each year and are analyzed and presented together in Figures 9 to 16. It must be emphasized that the data do not distinguish between activity without location changes and activity accompanied by movement.

Briefly, the data show a reduction in daytime activity of males during spring and summer months (Table 6) but an increase for females for the same periods (Table 7). Amplitude of activity during major activity periods for both males and females was higher from May to September than during other months of the non-winter denning period.

A more detailed analysis of activity data for 1968 was undertaken with a series of computer programs developed by the Chronobiology Laboratories of the University of Minnesota (Halberg, 1969). These programs determine the periods, level and time of peak activity (acrophase) by a least-squares fit of a 24-hour cosine function to data for each animal for each time period. The results of this analysis are not directly comparable to the extended activity analysis presented above since the temporal distribution of radio-tracked skunks did not permit the use of the same tracking periods (Table 8).

Figure 9. Activity patterns of male striped skunks during
March and April.

Figure 10. Activity patterns of female striped skunks
during March and April.

Figure 11. Activity patterns of male striped skunk
during May and June.

Figure 12. Activity patterns of female striped skunks
during May and June.

Figure 13. Activity patterns of male striped skunks during
July, August and September.

Figure 14. Activity patterns of female striped skunks
during July, August and September.

Figure 15. Activity patterns of male striped skunks
during October and November.

1201-68

1207-68

1217-68

1217-69

1235-68

1273-69

sunrise sunset

sunrise sunset

Figure 16. Activity patterns of female striped skunks
during October and November.

1213 - 69

1232 - 68

1233 - 68

1242 - 69

1269 - 69

1271 - 69

sunrise

sunset

sunrise

sunset

Table 6. Summary of activity pattern characteristics of male striped skunks. X's indicate the relative degree of the phenomenon.

	Period			
	March April	May June	July August September	October November
Level during major activity period	XX	XXX	XXX	Highly variable
Daytime activity	XXX	X	XX	Highly variable
Abrupt onset and cessation of activity	No	Yes	Yes	No
Onset and cessation closely synchronized w/sunrise and sunset	XX	X	X	X

Table 7. Summary of activity pattern characteristics of female striped skunks. X's indicate the relative degree of the phenomenon.

	Period			
	March April	May June	July August September	October November
Level during major activity period	XX	XXX	XXX	X
Daytime activity	X	XX	XXX	X
Abrupt onset and cessation of activity	Yes	No	Yes	No
Onset and cessation closely synchronized with sunrise, sunset	XX	XX	X	X

✓

Table 8. Cosine analysis value for skunk activity data for 1968.

Animal	Date (Period)	Rhythm detection (P)	Period (hours)	Level (.95 confidence interval)	Acrophase (Hours)
1201 ♂	6 April-14 June (1)	.01	24.00	1.90 (1.87 to 1.93)	2338 (2323 to 2357)
1204 ♀	6 April-19 June (1)	.01	23.99	1.95 (1.93 to 1.97)	2139 (2123 to 2156)
1207 ♂	6 April-19 June (1)	.01	24.01	1.90 (1.88 to 1.92)	2317 (2306 to 2328)
1217 ♂	6 April-14 June (1)	.01	23.99	1.90 (1.86 to 1.94)	2350 (2327 to 0014)
1201 ♂	1 July-6 Sept (2)	.01	23.99	1.94 (1.89 to 1.99)	0017 (2350 to 0044)
1217 ♂	1 July-6 Sept (2)	.01	24.03	2.22 (2.18 to 2.26)	0033 (0008 to 0058)
1232 ♀	1 July - 6 Sept (2)	.01	24.03	2.43 (2.41 to 2.45)	2318 (2252 to 2343)
1233 ♀	1 July-6 Sept (2)	.01	24.07	2.02 (1.98 to 2.06)	2324 (2257 to 2350)
1235 ♂	7 July-6 Sept (2)	.01	23.99	2.18 (2.14 to 2.22)	2310 (2240 to 2340)
1201 ♂	21 Sept-29 Nov (3)	.01	24.02	1.87 (1.82 to 1.92)	2357 (2331 to 0022)
1217 ♂	21 Sept-29 Nov (3)	.01	24.00	2.09 (2.05 to 2.13)	0004 (2340 to 0029)
1232 ♀	21 Sept-29 Nov (3)	.01	23.94	2.37 (2.33 to 2.41)	2258 (2147 to 0010)
1233 ♀	21 Sept-29 Nov (3)	.01	23.99	1.75 (1.71 to 1.79)	2336 (2306 to 0007)
1235 ♂	21 Sept-29 Nov (3)	.01	23.99	2.11 (2.07 to 2.15)	2330 (2308 to 2351)

When radio-locations were sampled (see Materials and Methods, p. 5) a signal indicating activity was given a number code 3; resting fixes were assigned code 1. To eliminate an either-or step function, the arithmetic mean of activity codes was computed for each animal for each hour. A cosine level of 2.00 would thus mean that activity occurred during one half of the total sampled intervals. A value less than or greater than 2.00 indicates that the animal was active during fewer and more than one-half of the total sampled intervals respectively (Table 8). The overall average level of activity for all animals was 1.91, 2.15, 2.03 for Periods 1 (March, April, May), 2 (June, July, August), and 3 (September, October, November). Levels of activity for both animals (1201, 1217) radio-tracked during all three periods were higher in Period 2 than Periods 1 or 3. Similarly, levels for all five animals radio tracked from July to November were higher during Period 2 than Period 3. These results are as expected since during the latter part of Period 3, striped skunks in Minnesota are beginning the winter dormancy state.

The period of the best cosine fit for all data closely approximated a true circadian rhythm (Table 8). There was some variation of the cosine period during Periods 2 and 3. This was especially pronounced for females in Period 2. The variation is probably related to increases in female daytime activity during this portion of the year.

Average acrophase for each period was 2308, 2348, and 2340 hours for Periods 1, 2 and 3, respectively. The disparity between Period 1 and Periods 2 and 3 resulted from a female whose acrophase occurred one and one-half hours earlier than the average for the group during Period 1. Acrophases for both 1201 and 1217 occurred later for Period 2 than for Periods 1 and 3. The acrophase of one additional animal (1232) that was radio-tracked only during Periods 2 and 3, was later in Period 2.

The data from Table 8 as well as the median day length for each period are summarized in graphic form in Figures 17 to 19.

Two hundred six dens and 183 aboveground rest sites were located during the course of this study. Underground dens comprised by far the greatest majority of dens (Figure 20).

Although the den type distribution is ultimately dependent upon the number of fallen trees, junk piles and buildings on the study area, the high percentage of underground dens seems to reflect a preference for that den type since many fallen trees, hollow logs and buildings were present but were not known to have been used by striped skunks. Individual preference varied markedly. Skunk 1201, for example, used hollow logs quite frequently. Other skunks did not use this type at all.

There was a distinct seasonal shift in the types of dens utilized by striped skunks (Figures 21, A, B). During the winter both sexes used underground dens almost exclusively

Figure 17. Cosine analysis of striped skunk activity data
for March, April and May 1968 (Period 1).

N OF SERIES IN SET= 00004

SET ACROPHASE (.95CI)= -347(0-21 -291)

SET AMPLITUDE (.95CI)= 1.03(.79 1.27)

SET LEVEL (.95CI)= 1.91(1.66 1.96)

CI=CONFIDENCE INTERVAL

NO POLE OVERLAP IF CONFIDENCE COEFFICIENT SMALLER THAN OR = .997

Figure 18. Cosine analysis of striped skunk activity data
for June, July and August 1968 (Period 2).

Figure 19. Cosine analysis of striped skunk activity data
for September, October and November 1968 (Period 3).

N OF SERIES IN SET: 00005

SET ACROPHASE (.95C11) = -355(00-4 -318)

SET AMPLITUDE (.95C11) = .841 .29 1.30

SET LEVEL (.95C11) = 2.03(1.56 2.50)

CI=CONFIDENCE INTERVAL

NO POLE OVERLAP IF CONFIDENCE COEFFICIENT SMALLER THAN OR = .994

Figure. 20. Types of dens used by striped skunks.

N = 206

Figure 21. Seasonal shift in den types, (A) males, (B) females.

Numbers in parentheses indicate sample sizes.

Numbers outside parentheses indicate the number of individual skunks in the sample.

— UNDERGROUND DENS
 --- ABOVE GROUND SITES
 - - - OTHER (HOLLOW LOGS,
 DEN TREES)

— UNDERGROUND DENS
 --- ABOVE GROUND SITES
 - - - OTHER (HOLLOW LOGS,
 DEN TREES)

but after emergence from the winter den both males and females began to use aboveground rest sites and hollow logs. Males continued to use these types throughout the spring and summer while females went back to underground dens during parturition and lactation. After the young began to travel with the female in late June and early July, both sexes used aboveground rest sites extensively. As winter approached both sexes began to use underground dens more and more frequently. These differences are best seen in Figure 22 where the seasonal percentages of underground dens for males and females are combined on one graph.

The sharp deflection on the curve for females (Figure 22) during May and June 1969 resulted from a female that was apparently not successfully bred until about 28 April. This animal continued to use aboveground rest sites during May but shifted to underground dens in June shortly before parturition.

The percentage of underground dens for each month was inversely related to the average monthly temperature (Figure 23, A, B). The correlation was higher for males ($r = -.84$) than for females ($r = -.55$) since females used underground dens during parturition and lactation (May and June) when the average monthly temperature was relatively high. No strong correlation existed between the percentage of underground dens and the total monthly precipitation for males ($r = -.33$) or females ($r = -.00$).

Figure 22. Seasonal shift in use of underground dens..

Figure 23. Percentage of underground dens in relation
to average monthly temperature (degrees
Fahrenheit), (A) males, (B) females.

Since the amount of moisture at dens and aboveground rest sites might be important in the maintenance and spread of diseases such as leptospirosis, habitats of all locations were classified as upland or lowland and were analyzed on a monthly basis.

There was a distinct seasonal shift of den habitat type for both males and females (Figure 24). Winter dens were almost exclusively in upland habitats while a significant proportion of summer rest sites was in lowland areas. Seasonal differences in den habitat usage between males and females were again related to parturition and lactation and resulted in a narrower time span in which females denned in moist lowland areas.

Habitat distributions for males and females were both related to the seasonal shifts in den types previously discussed, since significantly more underground dens were located in upland than in lowland habitats ($\chi^2 = 20.6$, 1 d.f.).

Multiple use of dens was minimal. Only 28 of 206 dens (Figure 25) and only 1 of 183 aboveground rest sites were used by two or more skunks simultaneously or consecutively. There was no significant difference in the frequency of multiple use for any den type ($\chi^2 = 5.85$, 4 d.f.). Despite the low incidence of multiple use there was a relatively high degree of intraspecific contact through communal and subsequent use of dens. Twenty-four and 17 radio-marked skunks had indirect and direct contact, respectively, with other radio-marked skunks (Figures 26 and 27). Communal denning occurred seasonally only from the third week in October through the first week of

Figure 24. Seasonal shift in den habitat types of striped
skunks.

Figure 25. Numbers of striped skunks known to have used
each den.

Figure 26. Number of striped skunks indirectly contacted
by sequential den use.

Figure 27. Number of striped skunks directly contacted
by simultaneous den use.

April. No males denned concurrently during this study but as many as six females were found with one male. Much individual variation occurred in the amount of denning contact. Some skunks had intraspecific denning contact with as many as nine animals. Others were not observed using a den that had been or was being occupied by another skunk. This variation might have been related in part to the distribution of radio-marked skunks on the study area. Trapping effort was concentrated near the radio-towers and thus the probability of trapping and relocating an individual was inversely related to its distance from the receiving antennae.

Monthly percentages of den changes between successive days were investigated by averaging radio locations for each of several skunks at 1100, 1200, and 1300 hours (C.S.T.). If the daily averaged bearings of one tower changed two or more degrees or if the bearings for each tower changed one or more degrees the animal was assumed to have switched den locations. These criteria were chosen because the overall accuracy of the tracking system and film reading is ± 1 degree. Occasional film reading errors of greater magnitude would tend to over-estimate the percentage of daily den changes but these should be counter balanced by underestimates resulting from den shifts of a distance insufficient to represent different degree bearings to the tracking system. There were very few den changes by males or females during the winter and by females immediately after parturition and lactation. After

the young began to travel with the females the family groups changed den locations about three out of four nights. Males changed dens very frequently from late winter through late autumn. The data were similar for all years and were pooled for analysis (Figure 28, A, B).

The average monthly distances between successive daily den locations were relatively constant throughout the year (Table 9). Males tended to move greater distances than females but the difference was not significant ($t = 0.86$; 22 d.f.). Individual variation was great. Some skunks moved as much as 1.71 miles between successive den sites.

Figure 28. Percentage of time striped skunks changed
successive den locations (A) males,
(B) females.

Table 9. Average monthly distances (miles) between successive den locations.

	Jan	Feb	Mar	April	May	June	July	Aug	Sept	Oct	Nov	Dec	$\bar{X}$
Males	-	.83	.34	.32	.31	.38	.35	.25	.18	.22	.21	.50	.33
Animals (Moves)	0(0)	1(1)	4(31)	5(59)	7(61)	6(34)	3(82)	6(46)	4(33)	6(67)	6(47)	2(5)	
Females	.27	.15	.18	.31	.42	.17	.31	.24	.22	.39	.16	.35	.27
Animals (Moves)	1(1)	1(3)	3(11)	6(52)	3(8)	1(10)	4(44)	4(48)	2(24)	6(36)	7(51)	4(6)	

DISCUSSION

Little work has been done on the movements or activity patterns of striped skunk. Verts' (1967) data were limited almost exclusively to juveniles and Storm and Verts (1966) tracked only one rabid juvenile skunk for a brief period. Certain comparisons can be made, however, between the results obtained in this investigation and the results of these early workers.

The marked variation in home range size observed in this study has been observed for various species (Ables, 1969; Storm, 1965). Verts (1967) found so much variation in the movements of individual striped skunks that he thought it inadvisable to attempt to draw boundaries on home ranges. This may or may not be a valid assessment. It is perhaps meaningless to determine an average home range size for animals in a given population, but some estimation of area covered can and must be made when attempting to answer certain biological questions. By limiting my analyses to those animals for which 850 or more locations had been determined, an estimate of range size and, hence, contact potential could be obtained.

Seasonal variation in home range size has been reported less frequently than individual variation since most investigators have tracked animals for only a short period of time. Verts (1967) attributed seasonal changes in movement patterns of skunks to food availability and reproductive condition. These factors

also seem to be involved in the present investigation. Food resources are at an annual low when skunks emerge from their winter dens in late February or early March. Both males and females are in generally poor condition at this time and must travel widely in search of food. Grasshoppers, one of the staple items of skunks' diets, do not become abundant until June or July and this scarcity is reflected in the movements of males during Periods 1 and 2. In addition, males are sexually active during March and April (Period 1). Verts (1967) found that adult males range one-half to one-fourth mile more nightly during the breeding season than juvenile males do in autumn.

Large seasonal ranges of females during July, August and September can also be explained on the basis of feeding patterns and reproductive conditions. Based on the average dates of parturition, females are bred in the winter den or shortly after emergence in early March. Due to the shortage of food and the rigors of pregnancy and lactation, females do not gain weight (except for that associated with pregnancy) until the end of lactation in June (Houseknecht, unpublished data). Weight gain of females is very rapid from July to October and this heavy feeding coupled with extensive movements of the family group results in large ranges at this time.

Several authors have linked food availability with movements of other species. Layne (1954) demonstrated that food supplies influenced the size and shape of home ranges of the red squirrel

(Tamiasciurus hudsonicus) and Turkowski and Mech (1966) suggested that raccoons (Procyon lotor) may shift ranges in response to food availability.

Verts (1967) found that the location of preferred hunting grounds in relation to the location of suitable dens appeared to be important factors in determining direction and extent of movements of juvenile striped skunks. This factor was of less importance in Minnesota because of a difference in study area habitat. Verts' (1967) research was conducted on an intensively cultivated area in northwest Illinois where suitable denning areas were quite limited. On CCNHA there are few cultivated fields and good denning areas are interspersed with good feeding sites.

Home range sizes of males and females were not directly comparable because of differences in the number of days radio tracked. When range size was computed as average square miles/100 days tracked, females appeared to have somewhat larger ranges than males. Evidence for other species indicates that males almost always have larger ranges than females. Mohr and Stumpf (1962) have shown that on an interspecific basis, large animals have larger home ranges and, as a result, a heavier ectoparasite load. Although no definite statements can be made, a large home range should increase the probability of direct contact with skunks as well as other species and the probability of indirect contact with vectors and vehicles (Ferris and Andrews, 1966).

Data on observed home range versus the number of days radio tracked suggest that either striped skunks do not have definite range limits or that these limits are obscured by periodic shifts of activity centers. Turkowski and Mech (1966) reported that one raccoon did not utilize the full extent of its range until five months had elapsed. They suggested that additional data for a later period might reveal additional extensions of range. Ables (1969) accumulated the daily ranges of red foxes (Vulpes vulpes) and felt that ranges had been adequately measured when the daily increase did not exceed one percent. This point was reached in most cases after about 18 days. Deer mice (Peromyscus leucopus), however, used their entire range each night (Sheppe, 1966).

Sheppe (1966) also observed that deer mice movement areas were decidedly linear with a statistical range of 1.3 to 5.3 units of length for each unit of width. Mohr and Stumpf (1962) suggested that a linear home range increases the number of habitats that will be sampled by the animal and the greater number of habitats traversed the greater will be the probability of contacting vector organisms.

Since location data were usually taken at equal intervals throughout the nightly activity periods, they represent an unbiased sample of the amount of time an animal spent in various areas during the active period. Data for all skunks showed that one or more area of the range was used more intensively than other areas. This same effect has been observed in virtually every species that has been investigated. Ables

(1969) found that ranges of red foxes contained areas of concentrated use to the extent that 22 percent of the area occupied contained 52 percent of the radio fixes and 57 percent of the area contained 84 percent of the fixes.

To my knowledge no one has attempted to determine theoretical contact between animals based on home range size or intensity of use. Jorgensen (1968) used activity centers and corresponding activity radii of mice to compute circular ranges and the interaction potential based on area overlap. But the method was not applicable to this study (and probably isn't to most) because it requires several assumptions that could not be met. First, it assumes that home ranges are circular and I have shown above that skunk ranges were decidedly linear. Second, the method assumes that there is a given probability of an animal being a certain distance from its activity center. Adult male 1201, for example, had two areas of high use intensity; one to the north and one to the south of the calculated center of activity. However, very few fixes fell directly to the west or east of the center and thus there was little probability that the animal would be found in these sectors.

Only Shirer and Fitch (1970) and Verts (1967) have investigated habitat preferences of striped skunks. Due to regional differences in habitat availability, their results are not directly comparable to mine; however, certain similarities do exist. The avoidance of upland wooded habitat by males

and lowland open habitat by both males and females can be explained on the basis of food availability. As mentioned previously, grasshoppers and other insects comprised a large portion of skunks' diets. Grasshoppers and beetles appeared to be much more numerous in upland open habitats (open fields and hedgerows) and, as expected, skunks utilized this type most intensively. Shirer and Fitch (1970) observed that skunks preferred grasslands but noted that opossums (Didelphis marsupialis), raccoons and skunks all fed around a small pond on their study area. Verts (1967) stated that skunks prefer open areas but he did not distinguish between upland and lowland habitat types. Turkowski and Mech (1966) reported feeding habits for a male raccoon which were similar to those observed for skunks in this study. Similarity in diets and preferred feeding areas would greatly increase the probability for direct and indirect interspecific contact between sympatric species.

The reduction of daytime activity of males during spring and summer seems to be associated with higher levels of feeding during activity periods and with plentiful food supplies. Similarly, the increase of daytime activity of females for the same period is related to parturition and the higher nutrient requirements during lactation. Several authors have suggested that skunks are almost never active in the daytime. Indeed, Parker (1962) suggests that seeing a skunk abroad during daylight hours in a rabies area is

sufficient to suggest that the animal is rabid. On the other hand, Verts (1967:44) occasionally observed skunks "during the daylight hours of early morning or late evening". On 25 April and 10 May 1968 I observed adult female 1205 feeding on grasshoppers in an open field at midday. On at least three other occasions females and their young were seen above ground during daylight hours.

The observed increase in the amplitude of major activity periods during summer suggests that, up to a point, skunks can meet their nutritional requirements by increasing their feeding activity during night time hours. When additional nutritative burdens are imposed, such as during lactation or periods of food shortage, daylight activity becomes necessary. Packer (1965) found that the quoka (Setonix brachyurus) increased its feeding activity when night length was short. He also found that daytime activity increased as the number of hours of darkness decreased. Similarly, Mech et al. (1966a) observed that the length of snowshoe hare (Lepus americanus) activity periods were directly correlated with the number of hours of darkness. Synchronization of activity periods on an interspecific or intraspecific basis increases the probability of direct contact. Also, daytime activity of skunks could be important in terms of contact with diurnal or crepuscular species.

Neither seasonal shifts in den types nor high use of aboveground dens has been reported previously for striped skunks. Shirer and Fitch (1970) and Selko (1938) studied the denning

habits of skunks during December, February, March and early April and spring, summer and fall respectively, but neither mentioned the use of aboveground dens. Verts (1967) reported that many juvenile striped skunks denned aboveground in waterways of corn fields during summer but none was known to have done so after mid-September. The high incidence of aboveground denning observed in this study would definitely reduce the amount of indirect and direct contact since no aboveground rest site was used concurrently by more than one animal and only one site was used sequentially by more than one skunk.

No previous worker has reported seasonal shifts in den habitat type by skunks due, I believe, to the lack of lowland cover in his study area. Turkowski and Mech (1966) observed that a raccoon shifted den locations from lowland areas in the spring, summer and fall to upland areas in the winter. Since in this study almost all lowland dens were aboveground, little direct or indirect contact would occur through concurrent or sequential use of dens. However, traveling to and from den sites in lowland areas could be important in contracting diseases such as leptospirosis which is transmitted by contact with infected urine under moist conditions.

Degree of indirect contact through sequential use of dens is dependent upon several factors including species using the area, abundance of suitable locations, patterns of den use and stability and permanence of dens. Kilgore (1969) found that swift fox (Vulpes velox) dens in Oklahoma disappeared between

spring and fall each year but Shirer and Fitch (1970:499) stated that "extensive and well situated dens are the communal property of the population and are relatively permanent so that they are used by successive generations" of raccoons, skunks and opossums. They recorded that one den had been in existence for at least 20 years and had been used by at least one red fox, four raccoons, three skunks and two opossums. Another den was used by four raccoons, one skunk and two opossums. Kilgore (1969) found many species (including striped skunks) in swift fox dens but did not indicate whether this represented sequential or concurrent use. Nine of 31 dens studied by Verts (1967) in 1960-61 were used by two or more species. Mead (1963) reported that a species of flea (Pulex simulans) was obtained by skunks from using dens that had previously been used by feral cats (Felis catus).

The low incidence of sequential den use in this study is biased in that I have no information on the number of dens actually entered by skunks. Other studies have shown that skunks often enter as many as five (Allen and Shapton, 1942) or seven (Ferris and Andrews, 1966) dens during a night's travel. Crabb (1948) suggested that the odor of one skunk might attract another skunk later.

Frequency of den changes of striped skunks is probably related to the number of suitable dens available. Verts (1967), working on an intensively cultivated area in northwestern Illinois, found that a male skunk used one den continuously

from 30 March to 23 April and alternated between this den and one other between 24 April and 2 May. Skunks on the University of Kansas Natural History Reservation (no cropland) changed dens on 57.6% of the nights during December, February, March and early April (Shirer and Fitch, 1970). A raccoon on CCNHA changed dens at least 80% of 99 nights (Turkowski and Mech, 1966).

I was unable to determine the number of times a skunk returned to (reused) a particular den because of the accuracy limitations of the tracking system. Two dens that were only a short distance apart might have resulted in the same degree bearings. However, Verts (1967) and Shirer and Fitch (1970) felt that skunks were strongly inclined to return to a previously used den.

The distance traveled between successive den locations affects how far and how quickly a disease organism might be spread. Shirer and Fitch (1970) reported a mean distance between successive den sites that is quite comparable to the mean of this study (1359 and 1584 feet, respectively). Their maximum record was 2660 feet, however, whereas in this study one skunk moved 1.71 miles (9029 feet). Verts (1967) recorded one movement of 1.63 miles (8606 feet) between successive den sites.

Results of this investigation indicate that, seasonally, there is a high degree of interspecific and intraspecific direct and indirect contact through concurrent use of dens. Numerous authors have reported intraspecific sharing of dens. Indeed, Seton (1926:357) found as many as one male and 20 females

in one den. Similarly, there are numerous reports of two or more species sharing a den. Shirer and Fitch (1970) found an adult female skunk with a sub-adult male opossum and Verts (1967) located a radio-marked skunk and a raccoon in the same den. Contact of this type is potentially very important because it may be one of the most effective means of transmitting certain disease organisms. For example, both tularemia (Kartman, et al., 1959) and rabies (Soave, 1966) can be transmitted by eating infected tissue. On at least two occasions I found skunk hair in scats dropped by a skunk which was sharing a den with other skunks. Allen and Shapton (1942) found one live skunk in a den with a dead skunk that had been partially eaten and Selko (1937) found skunk hair in a skunk scat in the fall.

Ferris and Andrews (1966) felt that communal occupancy of dens by a number of animals was an effective means of transmitting leptospirosis. Verts (1967:37) implies that breeding takes place within the winter den and states (p. 36) that before copulation the male licks the vulva of the female. In addition, he states (p. 172) that during copulation or attempted copulation females are almost invariably bitten by males and that the females often reciprocate. These activities would seem to provide an excellent opportunity for direct transmission of leptospirosis and rabies within the winter den. It is interesting to note that Ferris and Andrews (1966) found the highest incidence of leptospirosis in Illinois skunks between December and March, the time of winter denning. In Minnesota this is also the period.

of maximal potential for contact among striped skunk populations (Fig. 29).

In conclusion, it appears that there is considerable exposure potential for disease transmission in striped skunk populations. This contact varies greatly on a seasonal basis and its importance can be measured only in terms of a particular host-parasite relationship. Elimination of a specific disease requires a detailed knowledge of the complex interrelationships between hosts, causative organisms and the environment. It is hoped that this investigation will contribute towards eventual elimination of skunk related zoonoses.

Figure 29. Seasonal contact potential for striped skunk populations. The degree of shading indicates the contact potential.

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