

## **EPIZOOTIOLOGY OF SKUNK RABIES IN NORTH AMERICA**

Authors: Gremillion-Smith, Catherine, and Woolf, Alan

Source: Journal of Wildlife Diseases, 24(4) : 620-626

Published By: Wildlife Disease Association

URL: <https://doi.org/10.7589/0090-3558-24.4.620>

---

The BioOne Digital Library (<https://bioone.org/>) provides worldwide distribution for more than 580 journals and eBooks from BioOne's community of over 150 nonprofit societies, research institutions, and university presses in the biological, ecological, and environmental sciences. The BioOne Digital Library encompasses the flagship aggregation BioOne Complete (<https://bioone.org/subscribe>), the BioOne Complete Archive (<https://bioone.org/archive>), and the BioOne eBooks program offerings ESA eBook Collection (<https://bioone.org/esa-ebooks>) and CSIRO Publishing BioSelect Collection (<https://bioone.org/csiro-ebooks>).

Your use of this PDF, the BioOne Digital Library, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at [www.bioone.org/terms-of-use](http://www.bioone.org/terms-of-use).

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.

---

BioOne is an innovative nonprofit that sees sustainable scholarly publishing as an inherently collaborative enterprise connecting authors, nonprofit publishers, academic institutions, research libraries, and research funders in the common goal of maximizing access to critical research.

## EPIZOOTIOLOGY OF SKUNK RABIES IN NORTH AMERICA

Catherine Gremillion-Smith and Alan Woolf

Cooperative Wildlife Research Laboratory and Department of Zoology,  
Southern Illinois University, Carbondale, Illinois 62801, USA

**ABSTRACT:** Public health surveillance data from the United States and Canada (1961 to 1982) were analyzed to determine if consistent temporal and spatial patterns in skunk rabies could be identified. Enzootic/epizootic rabies was recognized in 18 states (enzootic states) based on the criteria of  $\geq 20$  yr of reported skunk rabies and at least 1 yr with a minimum of 50 reported rabid skunks. In other wildlife species, epizootics have been demonstrated to expand along a wave-like front. We hypothesized: if skunk rabies behaved in a similar fashion, states reporting rabid skunks would change over time. No such change was noted. During epizootics the number of counties reporting increased but not the number of states. Within Illinois certain counties were demonstrated to have persistent rabies histories and likely served as enzootic foci. Enzootic states combined prevalence indicated a 6 to 8 yr cycle for epizootics. Data on monthly percent rabies positive (number rabid/total number tested) were available from six states and Canada. Mean distributions were bimodal with winter and spring peaks. The patterns identified for skunk rabies differ from those of other major wildlife vectors and have significance for potential vaccination control regimes.

**Key words:** Rabies, skunks, epizootiology, surveillance data, enzootic rabies, epizootic rabies, geographic dispersal, *Mephitis mephitis*.

### INTRODUCTION

Since 1961, skunks are the most frequently reported rabid animal in North America (Winkler, 1986). However, in contrast to fox rabies that also occurs in Europe and Asia, the epizootiology of skunk rabies has not been as thoroughly studied (Carey and McLean, 1983). With rabies control likely because of recent efforts aimed at development of a safe oral vaccine for wildlife (Baer, 1985; Moser, 1985), it is critical that the epizootiology of rabies in each reservoir species be understood.

### MATERIALS AND METHODS

We recognize the unreliable nature of Public Health surveillance data on skunk rabies (Prior, 1969; Lewis, 1972; Rakowski and Andrews, 1972; Carey et al., 1978; Heidt et al., 1982; Carey and McLean, 1983). As Carey (1985) pointed out, submission policies are highly variable among states. A common policy is to test only those animals that have potentially exposed man and/or domestic animals; under such policies the true prevalence of rabies is probably underestimated (Macdonald, 1980). Few objective, long-term, field studies have been conducted especially during inter-epizootic periods (Carey, 1985). In spite of its limitations, surveillance data has been frequently used in sylvatic rabies research (Macdonald, 1980). Herein, we use surveillance data

to identify strong epizootiologic trends, that is, epizootiological patterns consistent throughout the various geo-political subdivisions of the study area.

There are six species of skunks in North America (Godin, 1982; Howard and Marsh, 1982; Jones et al., 1982). Public health surveillance data seldom distinguishes skunks according to species. The hog-nosed skunk (*Conepatus mesoleucus*), eastern hog-nosed skunk (*Conepatus leuconotus*) and hooded skunk (*Mephitis macroura*) have a limited distribution and occur in only one of the states included in this study, Texas. Spotted skunks (*Spilogale gracilis* and *S. putorius*) have a wide distribution but because of their lower densities and more secretive nature they are not considered to be principal vectors of rabies (Heidt et al., 1982; Pool and Hacker, 1982). The striped skunk (*Mephitis mephitis*) is widely distributed and numerous, and is believed to be the species most often reported rabid (Parker, 1975; Heidt et al., 1982; Pool and Hacker, 1982; Macdonald and Voigt, 1985).

Prior to 1961 and widespread use of the fluorescent antibody test, rabies diagnostic methods varied; therefore, for standardization only data collected after 1960 was used. National and state annual totals, and number of states and counties reporting rabid skunks were obtained from Annual Rabies Summaries published by the Centers for Disease Control (Centers for Disease Control, U.S. Department of Health and Human Services, Atlanta, Georgia 30333, USA). Eighteen states, hereafter referred to as enzootic states, were identified as having a significant

skunk rabies problem during 1961 to 1982 based on the occurrence of  $\geq 20$  yr with at least one rabid skunk and at least one annual total of reported skunk rabies of  $\geq 50$ . The Public Health Veterinarian or equivalent officer for each enzootic state was requested to furnish the following information: (1) The number of rabid skunks, by county; (2) The total number of rabid and non-rabid skunks examined annually; (3) The number of rabid and non-rabid skunks examined, monthly; and (4) Any annual reports, references, or other data. Similar data was obtained from Canada (Brian Jamison, Animal Health Division, Ottawa, Ontario, Canada K1A 0Y9). Complete data were available from Illinois, Iowa, North Dakota, South Dakota, Tennessee, and Texas. Partial data sets were received from Arkansas, California, Indiana, Kansas, Kentucky, Michigan, Missouri, Nebraska, Ohio, and Wisconsin. Data were not received from Minnesota and Oklahoma.

The national total reported rabid skunks and number of states and counties reporting were plotted for each year of the study period. Correlations between annual states and counties reporting and annual totals were determined by Pearson Product Moment Correlation (Helwig and Council, 1979). The annual skunk rabies distributions of the United States and Canada were plotted and compared. Individual state's annual reported and percent positive rates (where available) were plotted and distributions visually inspected to assess similarities and determine cyclic trends. To further explore cyclic trends, annual reports of skunk rabies were summed for the enzootic states, normalized by log transformation (base 10), and subjected to Time Series Analysis (International Business Machine Corporation, 1973; Poole, 1974).

Because of Illinois's history of enzootic/epizootic skunk rabies and the availability of a complete data set, it was chosen for in-depth analysis. The annual prevalence of reported skunk rabies for each county ( $n = 102$ ) was examined from 1961 to 1983. Prevalence of skunk rabies in each county was defined as total number of rabid skunks reported, 1961 to 1982. To reduce bias in prevalence that may have been due to aggressive reporting or easier access to testing facilities, percent positive (number of rabid skunks/total number of skunks submitted for testing) was calculated for each county's peak years. Rabies persistence was measured as the number of years at least one rabid skunk was reported. Counties with a prevalence  $\geq 20$ , percent positive  $\geq 50$  and persistence  $\geq 15$  yr were designated enzootic.

Spillover of rabies from its principal regional vector into other species during epizootics has been recognized as a common phenomenon

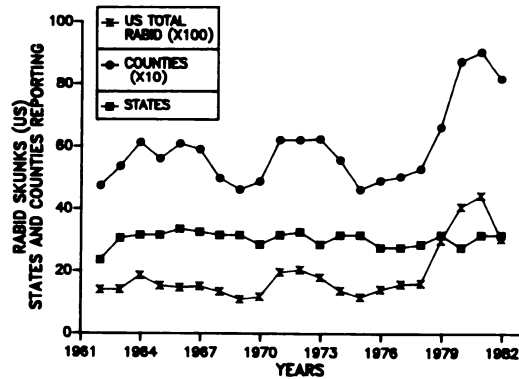


FIGURE 1. Annual totals, number of counties reporting at least one rabid skunk and number of states reporting rabies in the United States 1962 to 1982.

(Centers for Disease Control, 1983; Carey, 1985; Smith et al., 1986). Because people have a natural tendency to avoid skunks, rabid or otherwise, an indirect measure of skunk rabies was based on spillover. Monoclonal antibody studies have indicated that bats have a very limited role in terrestrial rabies (Centers for Disease Control, 1985; Smith et al., 1986). Therefore, counties reporting  $\geq 5$  rabid domestic and/or wildlife species other than bats or skunks were designated as "spillover" counties.

The distribution of Illinois's mean monthly number positive was visually compared to its distribution of mean monthly percent positive. Monthly percent positive data available from six states and Canada was plotted and their distributions were compared.

## RESULTS

The number of all states reporting rabid skunks ranged from 24 to 34. There was no clear association between the number of states and the annual totals ( $r = 0.04$ ,  $P = 0.86$ ) (Fig. 1). However, when the annual totals increased so did the number of counties ( $r = 0.94$ ,  $P = 0.0001$ ) (Fig. 1). For example, in 1975, 32 states reported 1,226 rabid skunks from 467 counties compared to 32 states reporting 4,480 rabid skunks from 907 counties in 1981.

Nationwide reported skunk rabies peaked in 1964, 1971–1972 and 1979–1981 (Fig. 1). Peaks in Canada tended to occur 1 yr after peaks in the United States. In the United States the number of reported rabid skunks increased with each out-

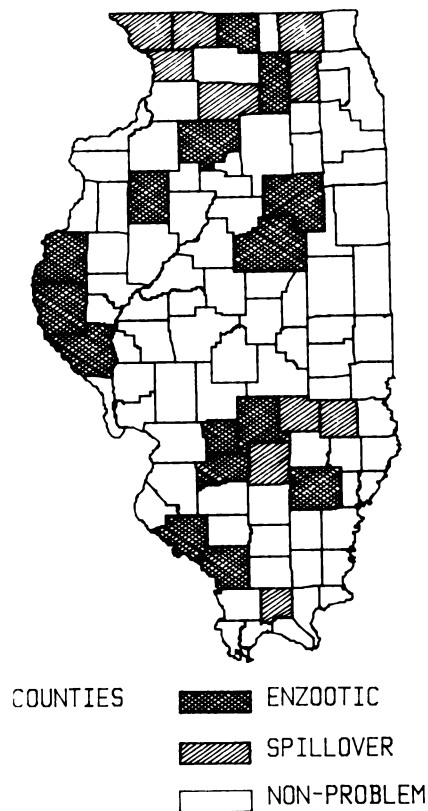


FIGURE 2. Skunk rabies enzootic, spillover and non-problem counties in Illinois. Enzoootic counties had  $\geq 50\%$  rabies positive during the last epizootic, and from 1961 to 1982 the occurrence of  $\geq 20$  rabid skunks and  $\geq 15$  years reporting at least one rabid skunk. Spillover counties reported  $\geq 5$  rabid animals other than skunks or bats during 1977 to 1984. Non-problem counties reported  $< 20$  rabid skunks from 1961 to 1982.

break; the annual total in 1981 (4,480) was over twice that of 1971 (2,095). The same trend was evident in Canada. Visual inspection of individual state and national distributions, and Time Series Analysis indicated a peak to peak reported rabies cycle of 6 to 8 yr.

Annual prevalence distribution in individual states was similar to the overall national patterns. Fourteen of the 18 enzootic states had a three peak pattern (mid-1960's, early 1970's and late 1970's and early 1980's). A progressive increase in magnitude of the peaks occurred in 14 of 18 states. Ten of 12 states showed a

concomitant increase in annual percent positive with increase in annual total positive.

Fifteen Illinois counties were designated enzootic and 20 counties spillover, including nine already designated enzootic (Fig. 2).

Comparison of the two monthly distributions in Illinois, mean monthly number positive and percent positive, demonstrated that these two measures of skunk rabies produce very different patterns (Fig. 3). Monthly percent positive was bimodal with spring and fall peaks whereas there was a single spring peak in monthly number positive. Distributions of monthly percent positive for the six states and Canada were bimodal with spring and late fall or early winter peaks (Figs. 3-6).

#### DISCUSSION

Monoclonal antibody studies have shown that the skunk rabies endemic area of North America had two separate origins (Smith et al., 1986). One virus strain has been associated with skunk rabies in the northern and eastern states, California, and Canada's prairie provinces and another with Texas and Kansas. Both virus strains are found in Missouri and Arkansas where the two epizootics are believed to have merged in the late 1960's (Centers for Disease Control, 1985). Rabid skunks in Ontario were not infected with either of the skunk strains; they exhibited the same strain as the rabid foxes in the province (Webster et al., 1985). Except for the situation in Ontario, virus isolate identification with monoclonal antibodies indicated endemic skunk rabies was maintained within a single species rather than a multi-species complex (Smith et al., 1986).

During the study period, skunk rabies did not exhibit wave-like propagation, except along a very limited front. Rather, skunk rabies persisted in limited endemic foci within the problem area and epizootics occurred as a result of increased prevalence within these foci and irregular centrifugal spread from them. In Illinois for

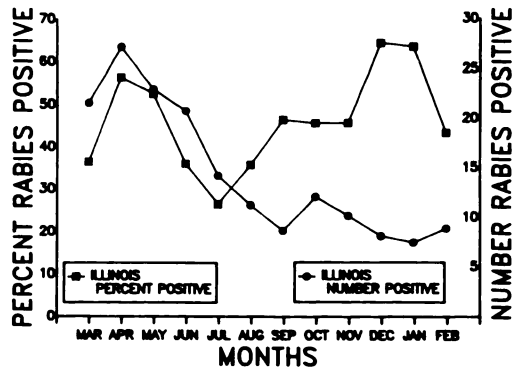


FIGURE 3. Monthly distribution of mean number (1964 to 1982) and mean percent rabies positive (1970 to 1983) reported skunk rabies cases for Illinois.

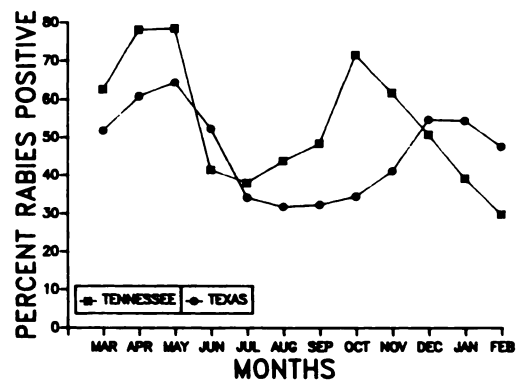


FIGURE 5. The distribution of mean monthly percent rabies positive submitted skunks for Tennessee (1974 to 1982) and Texas (1961 to 1977).

example, the enzootic and spillover counties were clumped (Fig. 2). Each clump represented an enzootic foci. During outbreaks the prevalence of rabies in the enzootic counties increased and more counties became involved. This same trend was true in other states. Comparison of the number of counties with the number of states reporting rabid skunks showed that during epizootics only the number of counties increased.

In Europe and Canada, fox (*Vulpes vulpes*) rabies has advanced over a wide geographic area along a wave-like front (Macdonald and Voigt, 1985). Raccoon (*Procyon lotor*) rabies has spread in a similar fashion through the mid-Atlantic States

(Centers for Disease Control, 1985). Fox rabies epizootics, in Europe and Canada, occurred as the front arrived in a rabies-free area and thereafter secondary peaks occurred at 3 to 5 yr intervals (Macdonald and Voigt, 1985). Macdonald and Voigt (1985) stated foci of enzootic rabies moved around, and nearby regions were out of phase with each other indicating that reintroduction from another region was probable. The near simultaneous occurrence of skunk rabies outbreaks in the enzootic states (for example California, Illinois, Iowa, Kansas, Minnesota, Nebraska, North Dakota, and Wisconsin all peaked in 1981 and the other states peaked in either 1979–1980 or 1982) makes it unlikely that out-

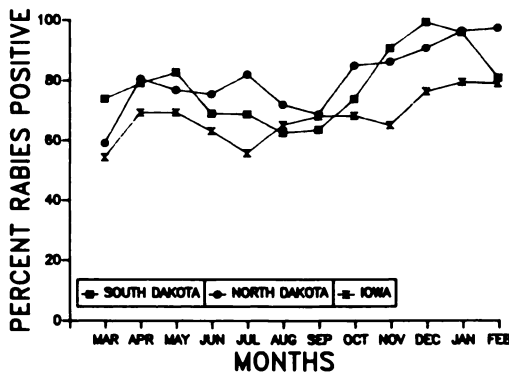


FIGURE 4. The distribution of mean monthly percent rabies positive submitted skunks for North Dakota (1977 to 1982), South Dakota (1977 to 1982) and Iowa (1979 to 1982).

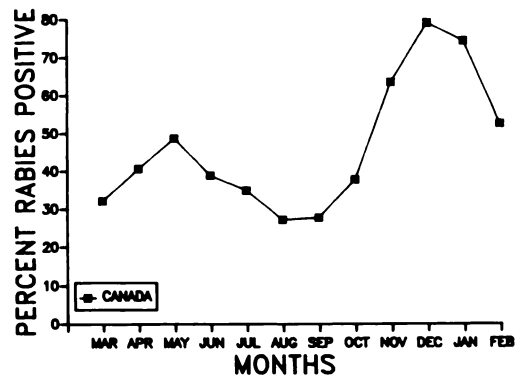


FIGURE 6. Distribution of mean monthly percent rabies positive submitted skunks for Canada (1977 to 1982).

breaks are the result of propagating infection from neighboring states. This is not to say rabies had not been invading new territory. Since 1959, skunk rabies had been invading the prairie provinces of Canada (Gunson et al., 1978). Recent increases in skunk rabies in the Dakotas and Montana have given the appearance of an additional westward spread (Winkler, 1986). However, rabid skunks have been reported from there since 1964. Therefore, during the study period the Saskatchewan and Alberta front was the only area in which skunk rabies advanced in a wave-like fashion into virgin territory.

Identification of an epizootic front, as is often possible with fox and raccoon rabies, can allow for a spatially and temporally restricted vaccination effort (Steck et al., 1982). Vaccinating hosts in front of the wave could create a barrier to continued spread, while the disease itself reduces the host population behind the wave to a level incapable of sustaining continued transmission. This strategy appears to have been successfully applied to halt an advancing wave of fox rabies in Switzerland (Steck et al., 1982). The same strategy, however, would not be useful against enzootic skunk rabies. Should a safe and effective oral vaccine be developed for skunk rabies, vaccination efforts would require identification of enzootic foci and elimination of the disease within.

Temporal patterns were fairly consistent across geo-political boundaries. The ascending three peak pattern was evident at state and national levels. The 6- to 8-yr cycle of skunk rabies was much longer than the 3-yr cycle reported for fox rabies in optimal habitat and the 4- to 5-yr cycle for areas of lower fox densities (Johnston and Beauregard, 1969). Verts (1967, p. 121) estimated that <25% of skunks survived their first year. Long interepizootic period and high population turnover are parameters likely to affect potential vaccination programs. During interepizootic periods the disease may persist in relatively small areas and vaccination efforts will have to

be thorough to eliminate it. In addition, vaccination will have to continue to insure immunity of each new generation of skunks.

Webster et al. (1974) and Gunson et al. (1978) stated the greatest number of rabid skunks were reported in early winter in Ontario and Saskatchewan, respectively, with a secondary peak in April. These authors commented on the absence of a winter peak in reported skunk rabies from the United States (Parker, 1961; Verts, 1967; Friend, 1968; Schnurrenberger et al., 1970). Schowalter and Gunson (1982) considered Canada's bimodal distribution with maximum numbers of rabid skunks occurring in the winter to be a distinguishing characteristic of northern skunk populations. Because mean monthly percent and number positive produced such different distributions (Fig. 3), we believe it is better to compare percent positive distributions; this measure reduces bias due to uneven submission rates. Comparison of percent positive distributions, from those states where data was available, demonstrated a more consistent bimodal pattern although there were differences in the magnitude of the winter and spring peaks. The pattern was less evident in North Dakota, which reported consistently high percent positive for all months (all months >50% and most >70%). Regrettably, this data was not available from more states. It would be interesting to compare annual distributions from states in southern climates where normal skunks are more likely to be active above ground throughout the winter, to those of northern climates states where skunks are largely confined to winter dens for prolonged periods. The greater percent rabid skunks in the winter in Canada, North Dakota, South Dakota, Iowa, and Illinois may reflect selection of abnormally behaving skunks; those above ground during the winter. However, this does not explain why the number of reported rabid skunks peaked in the winter in Canada but not in the United States. The likelihood of a rabid skunk being en-

countered may be a function of their distribution relative to humans. In the winter, skunks in Canada's prairie provinces concentrate near areas of high human activity such as graineries and farm buildings (Hayles and Dryden, 1970; Gunson and Bjorge, 1979; Andersen, 1981; Schowalter and Gunson, 1982), increasing the chance of a skunk being captured and submitted for rabies testing at this time of year.

It has been proposed that the annual pattern of reporting of skunk rabies is due to consistent life history events in populations that affect contact rate. Several investigators (Verts, 1967; Houseknecht, 1969; Webster et al., 1974; Parker, 1975; Gunson et al., 1978) have related peaks in reported skunk rabies to skunk activities. The spring peak is believed to be a result of increased contact during the breeding season and winter denning coupled with a delay due to the incubation period (Parker, 1961; Verts, 1967; Schnurrenberger et al., 1970). The winter peak has been related to increased contact between skunks during the fall dispersal of naive, susceptible juveniles (Webster et al., 1974; Gunson et al., 1978). More insight into annual patterns of skunk rabies could be gained if more states reported both monthly number and percent rabies positive.

#### SUMMARY

We have reviewed available public health surveillance data on skunk rabies in North America and identified some strong, consistent spatial and temporal patterns. The consistency of these patterns across North America was surprising in view of the varying regional influences such as different virus strains and presence or absence of other significant vectors. Skunk rabies was enzootic in the middle United States, California and most of southern Canada. Within this broad area it persisted in enzootic foci and erupted approximately every 6 to 8 yr. Outbreaks involved increase prevalence within the enzootic foci and additional areas. Skunk rabies peaked in the spring and again in the early winter.

These peaks may be attributed to the timing of certain life history events within skunk populations that promote increased contact and therefore increased disease transmission. There are marked differences between skunk and fox rabies epizootiology especially in the timing of outbreaks and the enzootic maintenance. If a safe oral vaccine is developed, proposed vaccination schemes would have to accommodate the unique nature of skunk rabies.

#### ACKNOWLEDGMENTS

We thank W. D. Klimstra, J. M. Martin and D. R. Voigt for reviewing this manuscript. We gratefully acknowledge the assistance of the public health veterinarians of the enzootic states who provided data. This research was supported by the Cooperative Wildlife Research Laboratory, Southern Illinois University at Carbondale.

#### LITERATURE CITED

- ANDERSEN, P. 1981. Movement, activity patterns and denning habitats of the striped skunk in the mixed grass prairie. M.S. Thesis. University of Calgary, Alberta, Canada, 221 pp.
- BAER, G. M. 1985. Wildlife control: New problems and strategies. In *World's debt to pasture*, H. Koprowski and S. Plotkin (eds.). Alan R. Liss, Inc., New York, New York, pp. 235-247.
- CAREY, A. B. 1985. Multispecies rabies in the eastern United States. In *Population dynamics of rabies in wildlife*, P. J. Bacon (ed.). Academic Press, London, England, pp. 23-41.
- , R. H. GILES, AND R. G. MCLEAN. 1978. The landscape epidemiology of rabies in Virginia. *American Journal of Tropical Medicine and Hygiene* 27:573-580.
- , AND R. G. MCLEAN. 1983. The ecology of rabies: Evidence of co-adaptation. *Journal of Applied Ecology* 20: 777-800.
- CENTERS FOR DISEASE CONTROL. 1983. Rabies surveillance annual summary 1980-1982. U.S. Department of Health and Human Services, Public Health Service, Atlanta, Georgia, 28 pp.
- . 1985. Rabies surveillance annual summary 1983. U.S. Department of Health and Human Services, Public Health Service, Atlanta, Georgia, 24 pp.
- FRIEND, M. 1968. History and epidemiology of rabies in wildlife in New York. *New York Fish and Game Journal* 15: 71-97.
- GODIN, A. J. 1982. Striped and hooded skunks. In *Wild mammals of North America*, J. A. Chapman and G. A. Feldhamer (eds.). Johns Hopkins University Press, Baltimore, Maryland, pp. 674-687.

- GUNSON, J. R., AND R. R. BJORGE. 1979. Winter denning of the striped skunk in Alberta. *Canadian Field-Naturalist* 93:252-258.
- , W. J. DORWARD, AND D. B. SCHOWALTER. 1978. An evaluation of rabies control in skunks in Alberta. *Canadian Veterinary Journal* 19: 214-220.
- HAYLES, L. B., AND I. M. DRYDEN. 1970. Epizootiology of rabies in Saskatchewan. *Canadian Veterinary Journal* 11: 131-136.
- HEIDT, G. A., D. V. FERGUNSON, AND J. LAMMERS. 1982. A profile of reported skunk rabies in Arkansas 1977-1979. *Journal of Wildlife Disease* 18: 269-277.
- HELWIG, J. T., AND K. A. COUNCIL (editors). 1979. SAS user's guide. SAS Institute Inc., Cary, North Carolina, 494 pp.
- HOUSEKNECHT, C. R. 1969. Denning habits of the striped skunk and the exposure potential for disease. *Bulletin of the Wildlife Disease Association* 5: 302-306.
- HOWARD, W. E., AND R. E. MARSH. 1982. Spotted and hog-nosed skunks. In *Wild mammals of North America*, J. A. Chapman and G. A. Feldhamer (eds.). Johns Hopkins University Press, Baltimore, Maryland, pp. 664-673.
- INTERNATIONAL BUSINESS MACHINES CORPORATION. 1973. Stat/basic program reference manual, 3rd ed. New York, New York, 220 pp.
- JOHNSTON, D. H., AND M. BEAUREGARD. 1969. Rabies epidemiology in Ontario. *Bulletin of the Wildlife Disease Association* 5: 357-370.
- JONES, J. K., JR., D. C. CARTER, H. H. GENOWAYS, R. S. HOFFMANN, AND D. W. RICE. 1982. Revised checklist of North American mammals north of Mexico, 1982. *Occasional Papers, The Museum, Texas Tech University* 80: 1-22.
- LEWIS, J. C. 1972. Factors influencing reports of rabid animals in Oklahoma. *Journal of Wildlife Diseases* 8: 245-250.
- MACDONALD, D. W. 1980. Rabies and wildlife; a biologist's perspective. Oxford University Press, New York, New York, 151 pp.
- , AND D. R. VOIGT. 1985. The biological basis of rabies models. In *Population dynamics of rabies in wildlife*, P. J. Bacon (ed.). Academic Press, London, England, pp. 71-108.
- MOSER, P. W. 1985. Rocky times for rocky. *Discovery* 6: 72-77.
- PARKER, R. L. 1961. Rabies in skunks in the north-central states. *Proceedings of the United States Livestock Sanitary Association* 65: 273-280.
- . 1975. Rabies in skunks. In *Natural history of rabies*, G. M. Baer (ed.). Academic Press, New York, New York, pp. 41-51.
- POOL, G. E., AND C. S. HACKER. 1982. Geographic and seasonal distribution of rabies in skunks, foxes and bats in Texas. *Journal of Wildlife Diseases* 18: 405-418.
- POOLE, R. W. 1974. An introduction to quantitative ecology. McGraw-Hill, New York, New York, 532 pp.
- PRIOR, E. T. 1969. A study of rabies incidence in western Virginia. M.S. Thesis. Virginia Polytechnic Institute, Blacksburg, Virginia, 57 pp.
- RAKOWSKI, P. W., AND M. F. ANDREWS. 1972. The geographic distribution of skunk rabies in North Dakota. *Proceedings of the North Dakota Academy of Science* 25: 65-71.
- SCHNURRENBERGER, P. R., R. J. MARTIN, AND J. M. KOCH. 1970. Rabies in Illinois skunks. *Journal of the American Veterinary Medical Association* 157: 1336-1342.
- SCHOWALTER, D. B., AND J. R. GUNSON. 1982. Parameters of population and seasonal activity of striped skunks, *Mephitis mephitis*, in Alberta and Saskatchewan. *Canadian Field-Naturalist* 96: 409-420.
- SMITH, J. S., F. L. REID-SANDEN, L. F. ROUNILLAT, C. TRIMARCH, K. CLARK, G. M. BAER, AND W. G. WINKLER. 1986. Demonstration of antigenic variation among rabies virus isolates by using monoclonal antibodies to nucleocapsid proteins. *Journal of Clinical Microbiology* 24: 573-580.
- STECK, F. A. WANDELER, P. BICHSEL, S. CAPT, U. HAFLIGER, AND L. SCHNEIDER. 1982. Oral immunization of foxes against rabies laboratory and field studies. *Comparative Immunology and Microbiology of Infectious Diseases* 5: 165-171.
- VERTS, B. J. 1967. The biology of the striped skunk. University of Illinois Press, Urbana, Illinois, 218 pp.
- WEBSTER, W. A., G. A. CASEY, K. M. CHARLTON, AND T. J. WIKTOR. 1985. Antigenic variants of rabies virus in isolates from eastern, central and northern Canada. *Canadian Journal of Comparative Medicine* 49: 186-188.
- , ———, H. TABEL, AND A. H. CORNOR. 1974. Skunk rabies in Ontario. *Canadian Veterinary Journal* 15: 163-167.
- WINKLER, W. G. 1986. Current status of rabies in the United States. In *Rabies concepts for medical professionals*, 2nd ed., D. B. Fishbein, L. A. Sawyer, and W. G. Winkler (eds.). Merieux Institute Inc., Miami, Florida, pp. 17-28.

Received for publication 25 August 1987.