

Rabies in Bats from Alabama

Authors: Hester, Laura C., Best, Troy L., and Hudson, M. Keith

Source: Journal of Wildlife Diseases, 43(2): 291-299

Published By: Wildlife Disease Association

URL: https://doi.org/10.7589/0090-3558-43.2.291

The BioOne Digital Library (<u>https://bioone.org/</u>) 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 (<u>https://bioone.org/subscribe</u>), the BioOne Complete Archive (<u>https://bioone.org/archive</u>), and the BioOne eBooks program offerings ESA eBook Collection (<u>https://bioone.org/esa-ebooks</u>) and CSIRO Publishing BioSelect Collection (<u>https://bioone.org/csiro-ebooks</u>).

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 <u>www.bioone.org/terms-of-use</u>.

Usage of BioOne Digital Library content is strictly limited to personal, educational, and non-commmercial 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.

Rabies in Bats from Alabama

Laura C. Hester,^{1,3} Troy L. Best,¹ and M. Keith Hudson² ¹ Department of Biological Sciences, 331 Funchess Hall, Auburn University, Alabama 36849, USA; ² Alabama Department of Conservation and Natural Resources, Division of Wildlife and Freshwater Fishes, 309 Knightsbridge Road, Florence, Alabama 35631, USA; ³ Corresponding author (email: hestelc@auburn.edu)

ABSTRACT: Data on rabies virus infection in bats that were submitted to the Alabama Department of Public Health from 1995-2005 were analyzed. Demographic factors, such as species and sex, and temporal aspects, such as yearly and monthly trends, were investigated. Thirteen species of bats were submitted, and of those, individuals from seven species were rabid; prevalence was highest in *Lasiurus* borealis and Pipistrellus subflavus and lowest in Eptesicus fuscus and Nycticeius humeralis. There was no difference in prevalence of rabies between sexes or years. Statistically, more rabid bats were submitted in August, September, and November; and fewer were submitted in March, June, and July. Results were similar to those from other regions of North America; these data from Alabama can help to present a more complete view of rabies in bats in North America.

Key words: Alabama, bats, Chiroptera, Molossidae, rabies, *Rhabdoviridae*, Vespertilionidae.

Most cases of rabies in the United States occur in wildlife (>91% in 2004), because most domestic animals are vaccinated (Krebs et al., 2005). Raccoons (*Procyon lotor*) are most frequently infected (37.5%), followed by skunks (27.1%; primarily the striped skunk, *Mephitis mephitis*), and bats (19.9%). Bats included at least 21 rabid species from 1993–2000 (Mondul et al., 2003; Krebs et al., 2005); other wildlife species contributed <10% of all cases of rabies in 2004 (Krebs et al., 2005).

Rabies virus was first identified in bats from the United States in the northern yellow bat (*Lasiurus intermedius*) from Florida in 1953 (Venters et al., 1954). Since that time, rabies has been detected in bats across the contiguous United States (Krebs et al., 2005). Prevalence of rabies in bats from the United States and Canada range from 2.4% to 15% (Table 1). These prevalence estimates may not accurately reflect the occurrence of rabies in these populations because they are derived from submissions to state health departments (Parker et al., 1999). Typically, <2% of free-flying bats are rabid (Venters et al., 1954; Girard et al., 1965; Trimarchi and Debbie, 1977; Constantine, 1988; Yancey et al., 1997).

Solitary species of bats frequently have a higher prevalence of rabies than colonial species (Table 1). Various explanations for this observation have been proposed, including sampling bias, aggressive behavior by solitary species, difference in genetic variant of rabies virus, and migrational stress (Rosatte, 1985; Childs et al., 1994; Parker et al., 1999). Evidence to support these hypotheses is somewhat contradictory in that the species with the second greatest prevalence, the Brazilian free-tailed bat (*Tadarida brasiliensis*), is a colonial species that is migratory throughout most of its range (Mondul et al., 2003). In addition, aggressive behavior by rabid individuals has been noted in a colonial species, the big brown bat (Eptesicus fuscus), whereas a solitary species, the eastern red bat (Lasiurus borealis) seems to be less aggressive than other species (Baer and Smith, 1991; Parker et al., 1999; Mondul et al., 2003). Although the observed prevalence of rabies in solitary species submitted for rabies examination is consistently greater than in colonial species, most cases of chiropteran rabies in the United States and Canada are found in E. fuscus (Pybus, 1986; Mondul et al., 2003).

Bats infected with rabies virus can infect humans if contact occurs. Although humans in the United States rarely are infected with rabies virus from any source, 28 of 31 cases of human rabies acquired in

Family	Species	Prevalence in Alabama	Prevalence reported in literature
Vespertilionidae	Corynorhinus rafinesquii ^a	0/2 (0%)	Arkansas (0%) ^c , Florida (0%), South Carolina (0%)
	Eptesicus fuscus ^a	22/372 (5.9%)	 Alberta (9.7%), British Columbia (25%), Arkansas (4.1%), Colo- rado (17%), Florida (0%), Georgia (0%), Illinois (3%), Indiana (3.7%), Manitoba (0%), Michigan (5.1%), Min- nesota (3.2%), New York (6.3%), Oklahoma (10.8%),Ontario (11.4%), Pennsylvania (4.7%), Sas- katchewan (3%), South Caro- lina (5%), Texas (7.1%)
	Lasiurus borealis ^b	51/300 (17.0%)	 Arkansas (17.4%), Tokas (117.6%) Arkansas (17.4%), Colorado (12%), Florida (5.9%), Georgia (15%), Illinois (5%), Indiana (7.1%), Manitoba (0%), Michigan (12.5%), Minnesota (0%), New York (4.8%), Oklahoma (8.8%), Ontario (20%), Pennsylvania (6.8%), South Carolina (18%), Texas (6.7%)
	Lasiurus cinereus ^b	0/18 (0%)	 Carolina (15%), Texas (6.7%) Alberta (24%), Arkansas (28%), Colorado (40%), Florida (16.6%), Georgia (20%), Illinois (11%), Indiana (19.6%), Manitoba (67%), Michigan (10%), Minnesota (20%), New York (10%), Oklahoma (37.5%), Ontario (33%), Pennsylvania (50%), South Carolina (13%), Texas (26.3%)
	Lasiurus intermedius ^b	0/2 (0%)	Florida (14.1%), South Carolina (0%), Texas (9.2%)
	Lasiurus seminolus ^b	23/201 (11.4%)	Florida (6.3%), Georgia (11%), South Carolina (13%), Texas (14.3%)
	Lasiurus spp. ^b	3/36 (8%)	
	Lasionycteris noctivagans ^b	0/6 (0%)	Alberta (2%), Arkansas (0%), Colorado (5%), Florida (0%), Georgia (0%), Illinois (4%), Indiana (0%), Manitoba (25%), Michigan (20%), Min- nesota (50%), New York (8%) Ontario (0%), Pennsylvania (0%), South Carolina (5%), Texas (0%)
	Myotis austroriparius ^a	0/6 (0%)	Arkansas (0%), Florida (1.7%), Georgia (16.6%), South Caro- lina (0%), Texas (0%)
	Myotis grisescens ^a	4/40 (10%)	Arkansas (8.3%), Georgia (0%), Oklahoma (0%)
	Myotis septentrionalis ^b	0/2 (0%)	Alberta (0%)

Family	Species	Prevalence in Alabama	Prevalence reported in literature
	Myotis spp.	0/9 (0%)	
	Nycteceius humeralis ^a	2/175 (1.1%)	Arkansas (2.7%), Georgia (1.2%) Illinois (2%), Indiana (0%), Michigan (0%), Oklahoma (0%), South Carolina (3%), Texas (0.7%)
	Pipistrellus subflavus ^b	12/55 (22%)	Arkansas (14.3%), Florida (3.9%) Georgia (0%), Indiana (12.5%), Manitoba (0%), New York (20%), Oklahoma (22.2%), Ontario (25%), Pennsylvania (20%), South Carolina (7%), Texas (0%)
Molossidae	Tadarida brasiliensisª	20/165 (12.1%)	Arkansas (3.6%), Colorado (12%), Florida (7.9%), Georgia (1.3%), Oklahoma (0%), South Carolina (9%), Texas (16.4%)
	Total solitary	89/620 (14.4%)	Alberta (8.3%), Florida (12.2%), Georgia (14%), Michigan (13%), Minnesota (20%), South Carolina (15.3%)
	Total colonial	48/760 (6.3%)	Alberta (3.8%), Florida (3.1%), Georgia (1.3%), Michigan (4.5%), Minnesota (2.5%), South Carolina (4.5%)
	Total	137/1,389 (9.9%)	 Alberta (4.6%), Arkansas (9.8%), Arizona (2.4%), British Co- lumbia (9.7%), Colorado (15%), Florida (10.3%), Geor- gia (6.7%), Illinois (6%), In- diana (5.1%), Kansas (10.8%), Michigan^d (6.2%), Minnesota (3.1%), New York (4.6%), Ok- lahoma (8.1%), Ontario (5.9%), Pennsylvania (3.9%), Saskatchewan (2.9%), South Carolina (9%), Texas (11%)

TABLE 1. Continued.

^a Colonial species.

^b Solitary species.

^c References unless otherwise indicated: Alberta (Rosatte, 1985), Arizona (Dean et al., 1960), Arkansas (Heidt et al., 1991), British Columbia (Pybus, 1986), Colorado (Pape et al., 1999), Florida (Bigler et al., 1975), Georgia (Richardson et al., 1966), Illinois (Burnett, 1989), Indiana (Whitaker and Miller, 1973), Kansas (Birney and Rising, 1967), Manitoba (Beauregard, 1969), Michigan (Kurta, 1979), Minnesota (Steece et al., 1982), New York (Childs et al., 1994), Oklahoma (Caire, 1998), Ontario (Beauregard, 1969), Pennsylvania (Wampler and Kirkland, 1981), Saskatchewan (Pybus, 1986), South Carolina (Parker et al., 1999), Texas (Rohde et al., 2004).

^d (Feller et al., 1997).

the United States from 1990 to 2003 were linked to genetic variants of rabies virus from bats (Krebs et al., 2004). Most of these cases (17/24 cases during1990–2000) were related to a specific variant found in silver-haired bats (*Lasionycteris noctivagans*) and eastern pipistrelles (*Pipistrellus* subflavus; Messenger et al., 2002; Mondul et al., 2003). Rabid bats of all species were most likely detected in autumn, but *L. noctivagans* and *P. subflavus* were more likely to be rabid if collected in summer (Mondul et al., 2003). In contrast, when sources of rabies infections of domestic animals in the United States were investigated, none of the 78 dogs and only 1 of 230 cats in 1999 had genetic variants of rabies virus that came from bats (McQuiston et al., 2001); the variant of rabies virus infecting the single cat was determined to be from *E. fuscus* (McQuiston et al., 2001).

Fifteen species of bats are native to Alabama, including: E. fuscus, L. noctivagans, L. borealis, Lasiurus cinereus, L. intermedius, Lasiurus seminolus, Myotis austroriparius, Myotis grisescens, Myotis lucifugus, Myotis septentrionalis, Myotis sodalis, Nycticeius humeralis, P. subflavus, Corynorhinus rafinesquii, and T. brasiliensis (Best, 2004). Individuals from 12 of these species, excluding M. septentrionalis, M. sodalis, and C. rafinesquii, have tested positive for rabies virus in the United States (Constantine, 1988). In this study, data from bats provided to Auburn University by the Alabama Department of Public Health from 1995 through 2005 were studied to elucidate epidemiology of chiropteran rabies in Alabama.

Bats submitted for rabies diagnosis to the Alabama Department of Public Health were provided to the authors with results of fluorescent antibody tests for rabies virus and dates of submission. Bats that were reported as not suitable for rabies diagnosis were excluded from this study. Species and sex identification were determined by one of the authors (TLB), and all bats were deposited in the museum of Auburn University. In most cases, L. borealis and L. seminolus could be identified, but 32 individuals were difficult to distinguish and were categorized as Lasiurus spp. For nine specimens of Myotis, it was not possible to determine species; thus, these were categorized as Myotis spp. Data were evaluated to detect possible relationships between infection by rabies virus and demographic and temporal aspects in populations of bats. Contingency tables were produced using SPSS statistical software (SPSS, 2004) to investigate trends in rabies in bats by year,

month, sex, and species. Adjusted residual (AR) absolute values of >1.96 were used to indicate a statistically significant difference using Pearson Chi-Squared values. Missing data for some specimens caused them to be removed from statistical analyses, but in all cases the sample consisted of \geq 94% of submitted bats.

From 1995 through 2005, 1,389 bats were obtained by Auburn University from the Alabama Department of Public Health, which included 13 of 15 native species (Table 1); 137 were rabid, for an overall prevalence of 9.86%. The most commonly submitted bats were *E. fuscus* (26.8%) and *L. borealis* (21.6%).

There was no significant difference in number of bats with rabies virus that were submitted during 1995-2005 (P > 0.05; Fig. 1). However, there was a significant difference in number of rabid bats submitted during different months of the year (Fig. 2). Numbers of rabid bats submitted in March (AR=-2.3), June (AR=-5.2), and July (AR = -2.4) were lower than predicted by the total number of submissions (P < 0.01). Additionally, more rabid bats were submitted in August (AR=6.0), September (AR=8.2), and November (AR=2.6; P<0.01). Seasonal trends for individual species did not differ from the combined species trends.

Of the bats for which sex was determined, there were 689 females and 618 males; of those, 61 females and 69 males were rabid. A difference in prevalence of rabies between sexes was not detected (P > 0.05) for the total sample or for individual species. However, there was a significant difference in rabies prevalence among species (Fig. 3). Prevalence of rabies in E. fuscus (5.9%, AR = -3.0)and N. humeralis (1.1%, AR = -4.1) was lower (P < 0.01) than prevalence for all bats. Conversely, prevalence was higher (P < 0.01) for L. borealis (17.0% rabid, AR=4.7) and P. subflavus (22% rabid, AR=3.0); L. borealis represented 37.2% of all rabid bats. When pooled, prevalence of rabies in noncolonial species (14.4%)



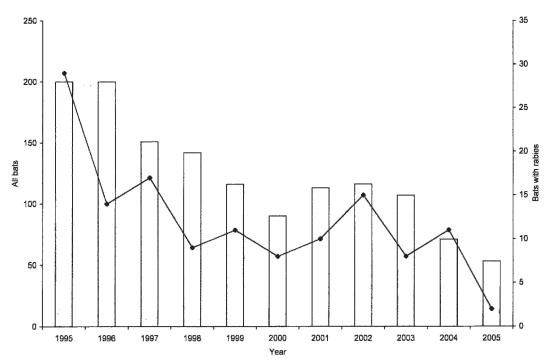


FIGURE 1. Annual distribution of submissions of bats and number of bats that tested positive for rabies virus in Alabama, 1995–2005.

was more than twice that of colonial species (6.3%).

Prevalence of rabies in Alabama is similar to those reported from other states and Canadian provinces (Table 1). Prevalence was <10% although bats were submitted based on a suspicion of rabies. Nationally, Myotis yumanensis and M. *lucifugus* had the lowest reported prevalences (1.7%) for both species; Mondul et al., 2003). In the present study, N. humeralis (1.1%) had the lowest prevalence, which is similar to results from other states (Table 1). Nationally, prevalences of rabies in L. cinereus and T. brasiliensis were greatest (38.2 and 31.8%, respectively; Mondul et al., 2003). In Alabama, however, T. brasiliensis did not have significantly higher (or lower) prevalence of rabies than other species and no rabid L. cinereus was detected. However, only 18 L. cinereus was submitted in our study over the 11-yr period (Table 1).

Alabama differs from other southeastern states in that E. fuscus was the most frequently submitted species (n=372), whereas L. borealis comprised the majority of submissions of bats in other southeastern states, including Arkansas, Georgia, and South Carolina (Richardson et al., 1966; Heidt et al., 1991, Parker et al., 1999). Eptesicus fuscus was submitted most often from other regions and the observed prevalence of rabies (5.9%) was similar to the national prevalence (5.8%; Mondul et al., 2003; Table 1). Prevalence of rabies virus for L. borealis in Alabama (17.0%) was greater than the national average (9.0%; Mondul et al., 2003; Table 1).

Prevalence of rabies was highest for noncolonial species, such as *L. borealis*; this result is consistent with results from other studies (Table 1). Likewise, for two solitary species, *P. subflavus* and *L. seminolus*, prevalences in Alabama (22%)



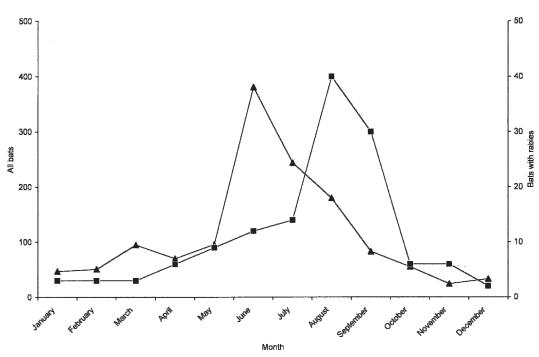


FIGURE 2. Monthly distribution of submissions of bats and number of bats that tested positive for rabies virus in Alabama, 1995–2005.

and 11.4%, respectively) were higher than reported for these species in other states (Table 1). For *P. subflavus*, prevalence also was higher than the national average (17.1%; Mondul et al., 2003). Two colonial species, *M. grisescens* and *T. brasiliensis* (10% and 12.1%, respectively in Alabama), also had prevalences greater than those reported from other states (Table 1), but prevalence for *T. brasiliensis* was lower than the national average (31.8%; Mondul et al., 2003).

In Alabama and New York, *P. subflavus* had the greatest prevalence, but in New York and other studies *P. subflavus* was considered a colonial species (Richardson et al., 1966; Bigler et al., 1975; Childs et al., 1994). The roosting behavior of *P. subflavus* is more comparable with solitary species such as members of the genus *Lasiurus*. *Pipistrellus subflavus* hibernates singly, and in summer, males and non-reproductive females roost singly in trees. The maternity colonies of reproductive

females consist of few individuals, unlike typical colonial species such as *E. fuscus* (Fujita and Kunz, 1984; Veilleux et al., 2003; Veilleux and Veilleux, 2004). Treating *P. subflavus* as a colonial species in analysis of solitary versus colonial pooled prevalence would not change the overall result. Reasons for the greater prevalence of rabies in solitary species are not clear, and a combination of factors such as sampling bias, behavioral differences, and genetic variants of rabies virus probably are responsible.

For the two species considered epidemiologically most important in transmission of rabies virus to humans, only *P. subflavus* tested positive in Alabama, but *L. noctivagans* was represented by only six individuals over 11 yr. These species are associated with a unique variant of rabies virus and with cases of rabies in humans where exposure to possible rabid animals was denied by the human (Mondul et al., 2003). Bat bites were reported in only one □All bats ■Bats with rabies

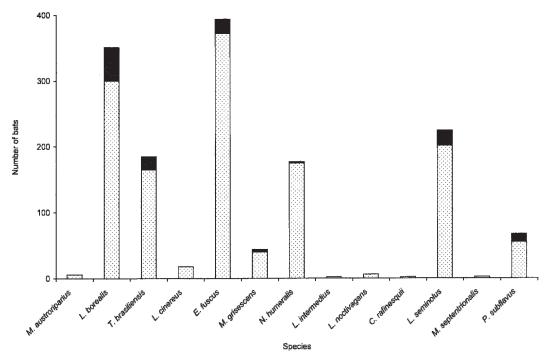


FIGURE 3. Total number of each species of bat submitted for diagnosis and number of bats with rabies virus in Alabama, 1995–2005.

of 22 cases of human rabies from 1981–98 where the virus variant was linked to bats (Krebs et al., 2000; Messenger et al., 2002). This variant of rabies virus might be able to replicate in epidermal tissue at a lower temperature, allowing minute amounts of virus associated with a scratch or bite to become established in a human host (Morimoto et al., 1996). The natural history of *P. subflavus* and *L. noctivagans*, and the fact that they comprise a minority of specimens submitted in Alabama (4.0%) and 0.4% of total submissions, respectively), suggests that they rarely come into contact with humans (Mondul et al., 2003).

Absence of a statistically significant difference in percentage of rabid bats between years (1995–2005) in this study implies that levels of rabies in bats remains stable in Alabama; this appears to be the case in other areas (Kurta, 1979; Steece et al., 1982; Olnhausen and Gannon, 2004; Rohde et al., 2004). However, temporal

distribution of rabid bats throughout the year varies among studies. A higher prevalence in autumn, as observed in Alabama, also was reported by other states, but in Illinois, Georgia, and South Carolina, an additional increase in cases of rabies was seen in spring (Richardson et al., 1966; Whitaker and Miller, 1973; Bigler et al., 1975; Kurta, 1979; Steece et al., 1982; Rosatte, 1985; Burnett, 1989; Childs et al., 1994; Parker et al., 1999). These increases most likely reflect behavioral patterns of common bat species with stress due to migration or newly volant young contributing to seasonal patterns. The lack of prevalence differences between sexes in Alabama was consistent with results reported from Alberta, Florida, and Minnesota, but contrasted with results from studies in New York and Illinois where females had greater prevalence of rabies and Oklahoma, where males had a higher prevalence (Bigler et al., 1975; Steece et al., 1982; Rosatte,

1985; Burnett, 1989; Childs et al.,1994; Caire, 1998).

Analysis of rabies in bats from Alabama has provided a more complete picture of the status of rabies in the United States. These results could help to shape future management plans for bats in the state, and provide information as to precautions for chiropterologists working in Alabama, as well as the general public. Although the risk of encountering a rabid bat in Alabama generally is <10%, biologists should exercise caution when working with bats, especially during autumn months. Additionally, data from submissions of bats not only provides information on rabies in Alabama but also the distribution of bats. Submission of two L. intermedius included in this study doubled the known specimens for the species in Alabama. Most importantly, work is needed to ensure that fear of rabies from bats does not endanger conservation efforts for these important mammals.

We thank personnel of the Alabama Department of Public Health for providing specimens and associated data, the numerous students who aided in recording data from specimens, and C. A. Sundermann, R. S. Lishak, and two anonymous reviewers for providing comments on drafts of the manuscript. This project was partially funded by the Alabama Agricultural Research Station, Auburn University.

LITERATURE CITED

- BAER, G. M., AND J. S. SMITH. 1991. Rabies in nonhematophagous bats. *In* The natural history of rabies, 2nd Edition, G. M. Baer (ed.), CRC Press, Boca Raton, Florida, pp. 341–366.
- BEAUREGARD, M. 1969. Bat rabies in Canada 1963– 1967. Canadian Journal of Comparative Medicine 33: 220–226.
- BEST, T. L. 2004. Mammals. In Alabama wildlife: A checklist of vertebrates and selected invertebrates: aquatic mollusks, fishes, amphibians, reptiles, birds, and mammals, R. E. Mirarchi (ed.). The University of Alabama Press, Tuscaloosa, Alabama, pp. 185–204.
- BIGLER, W. J., G. L. HOFF, AND E. E. BUFF. 1975. Chiropteran rabies in Florida: A twenty-year

analysis, 1954 to 1973. The American Journal of Tropical Medicine and Hygiene 24: 347–352.

- BIRNEY, E. C., AND J. D. RISING. 1967. Notes on distribution and reproduction of some bats from Kansas, with remarks on prevalence of rabies. Transactions of the Kansas Academy of Science 70: 519–524.
- BURNETT, C. D. 1989. Bat rabies in Illinois: 1965 to 1986. Journal of Wildlife Diseases 25: 10–19.
- CAIRE, W. 1998. Rabies in bats from Oklahoma. Proceedings of the Oklahoma Academy of Science 78: 59–65.
- CHILDS, J. E., C. V. TRIMARCHI, AND J. W. KREBS. 1994. The epidemiology of bat rabies in New York State, 1988–92. Epidemiology and Infection 113: 501–511.
- CONSTANTINE, D. G. 1988. Health precautions for bat researchers. In Ecological and behavioral methods for the study of bats, T. H. Kunz (ed.). Smithsonian Institution Press, Washington, D.C., pp. 491–528.
- DEAN, W. D., K. T. MADDY, E. L. COCKRUM, AND H. G. CRECELIUS. 1960. Rabies in insectivorous bats of Arizona. Arizona Medicine 17: 69–77.
- FELLER, M. J., J. B. KANEENE, AND M. G. STOBIERSKI. 1997. Prevalence of rabies in bats in Michigan, 1981–1993. Journal of the American Veterinary Medical Association 210: 195–200.
- FUJITA, M. S., AND T. H. KUNZ. 1984. Pipistrellus subflavus. Mammalian Species 228: 1–6.
- GIRARD, K. F., H. B. HITCHCOCK, G. EDSALL, AND R. A. MACCREADY. 1965. Rabies in bats in southern New England. The New England Journal of Medicine 272: 75–80.
- HEIDT, G. A., D. A. SAUGEY, L. CHANDLER, AND K. D. STONE. 1991. Reported animal rabies in Arkansas: 1982–1990. Proceedings Arkansas Academy of Science 45: 41–45.
- KREBS, J. W., J. S. SMITH, C. E. RUPPRECHT, AND J. E. CHILDS. 2000. Mammalian reservoirs and epidemiology of rabies diagnosed in human beings in the United States, 1981–1998. Annals of the New York Academy of Sciences 916: 345–353.
 - —, E. J. MANDEL, D. L. SWERDLOW, AND C. E. RUPPRECHT. 2004. Rabies surveillance in the United States during 2003. Journal of the American Veterinary Medical Association 225: 1837–1849.
- , _____, ____, AND _____. 2005. Rabies surveillance in the United States during 2004. Journal of the American Veterinary Medical Association 227: 1912–1925.
- KURTA, A. 1979. Bat rabies in Michigan. Michigan Academician: Papers of the Michigan Academy of Science, Arts, and Letters 12: 221–230.
- MCQUISTON, J. H., P. A. YAGER, J. S. SMITH, AND C. E. RUPPRECHT. 2001. Epidemiologic characteristics of rabies virus variants in dogs and cats in the United States, 1999. Journal of the American Veterinary Medical Association 218: 1939–1942.

- MESSENGER, S. L., J. S. SMITH, AND C. E. RUPPRECHT. 2002. Emerging epidemiology of bat-associated cryptic cases of rabies in humans in the United States. Clinical Infectious Diseases 35: 738–747.
- MONDUL, A. M., J. W. KREBS, AND J. E. CHILDS. 2003. Trends in national surveillance for rabies among bats in the United States (1993–2000). Journal of the American Veterinary Medical Association 222: 633–639.
- MORIMOTO, K., M. PATEL, S. CORISDEO, D. C. HOOPER, Z. F. FU, C. E. RUPPRECHT, H. KOPROWSKI, AND B. DIETZSCHOLD. 1996. Characterization of a unique variant of bat rabies virus responsible for newly emerging human cases in North America. Proceedings of the National Academy of Sciences of the United States of America 93: 5653–5658.
- OLNHAUSEN, L. R., AND M. R. GANNON. 2004. An evaluation of bat rabies prevention in the United States, based on an analysis from Pennsylvania. Acta Chiropterologica 6: 163–168.
- PAPE, W. J., T. D. FITZSIMMONS, AND R. E. HOFFMAN. 1999. Risk for rabies transmission from encounters with bats, Colorado, 1977–1996. Emerging Infectious Diseases 5: 433–437.
- PARKER, E. K., H. DOWDA, S. E. REDDEN, M. W. TOLSON, N. TURNER, AND W. KEMICK. 1999. Bat rabies in South Carolina, 1970–90. Journal of Wildlife Diseases 35: 557–564.
- PYBUS, M. J. 1986. Rabies in insectivorous bats of western Canada, 1979 to 1983. Journal of Wildlife Diseases 22: 307–313.
- RICHARDSON, J. H., R. L. RAMSEY, AND L. E. STARR. 1966. Bat rabies in Georgia, 1956–65. Public Health Reports 81: 1031–1035.
- ROHDE, R. E., B. C. MAYES, J. S. SMITH, AND S. U. NEILL. 2004. Bat rabies, Texas, 1996–2000. Emerging Infectious Diseases 10: 948–952.

- ROSATTE, R. C. 1985. Bat rabies in Alberta 1979– 1982. The Canadian Veterinary Journal 26: 81– 85.
- SPSS. 2004. SPSS[®] Base 13.0 User's Guide., SPSS, Inc, Chicago, Illinois, 712 pp.
- STEECE, R. S., T. J. ERICKSON, AND R. A. SIEM. 1982. Chiropteran rabies in Minnesota: 1976–1980. Journal of Wildlife Diseases 18: 487–489.
- TRIMARCHI, C., V., AND J. G. DEBBIE. 1977. Naturally occurring rabies virus and neutralizing antibody in two species of insectivorous bats of New York State. Journal of Wildlife Diseases 13: 366–369.
- VEILLEUX, J. P., AND S. L. VEILLEUX. 2004. Intraannual and interannual fidelity to summer roost areas by female eastern pipistrelles, *Pipistrellus subflavus*. American Midland Naturalist 152: 196–200.
- —, J. O. WHITAKER, JR., AND S. L. VEILLEUX. 2003. Tree-roosting ecology of reproductive female eastern pipistrelles, *Pipistrellus subflavus*, in Indiana. Journal of Mammalogy 84: 1068–1075.
- VENTERS, H. D., W. R. HOFFERT, J. E. SCATTERDAY, AND A. V. HARDY. 1954. Rabies in bats in Florida. American Journal of Public Health 44: 182–185.
- WHITAKER, J. O., JR, AND W. A. MILLER. 1973. Rabies in bats of Indiana: 1968–1972. Proceedings of the Indiana Academy of Science 83: 469–472.
- WAMPLER, J. T. II, AND G. L. KIRKLAND, JR. 1981. Rabies in Pennsylvania. Proceedings of the Pennsylvania Academy of Science 55: 47–51.
- YANCEY, F. D., P. RAJ, S. U. NEILL, AND C. JONES. 1997. Survey of rabies among free-flying bats from the big bend region of Texas. Occasional Papers, Museum of Texas Tech University 165: 1–5.

Received for publication 3 March 2006.