Epidemiol. Infect. (1994), **113**, 501–511
Copyright © 1994 Cambridge University Press

The epidemiology of bat rabies in New York State, 1988–92

J. E. CHILDS,[1] C. V. TRIMARCHI[2] AND J. W. KREBS[1]

[1] *Viral and Rickettsial Zoonoses Branch, Centers for Disease Control and Prevention, MS G13, 1600 Clifton Road, Atlanta, GA 30333, USA*

[2] *Wadsworth Center for Laboratories and Research, New York State Department of Health, Albany, NY 12201*

(*Accepted 14 July 1994*)

SUMMARY

In 1993 New York and Texas each reported a human rabies case traced to a rare variant of rabies virus found in an uncommon species of bat. This study examined the epidemiology of bat rabies in New York State. Demographic, species, and animal-contact information for bats submitted for rabies testing from 1988–92 was analysed.

The prevalence of rabies in 6810 bats was 4·6%. Nearly 90% of the 308 rabid bats identified to species were the common big brown bat (*Eptesicus fuscus*), which comprised 62% of all submissions. Only 25 submissions were silver-haired bats (*Lasionycterus noctivagans*), the species associated with the two 1993 human cases of rabies, and only two of these bats were positive. Rabies was most prevalent in female bats, in bats submitted because of human or animal contact, and in animals tested during September and October.

These results highlight the unusual circumstances surrounding the recent human rabies cases in the United States. A species of bat rarely encountered by humans, and contributing little to the total rabies cases in bats, has been implicated in the majority of the indigenously acquired human rabies cases in the United States. The factors contributing to the transmission of this rare rabies variant remain unclear.

INTRODUCTION

In July 1993, an 11-year-old girl died of rabies in New York State [1]. The girl had no history of rabies exposure either through bite or other contact with a suspected rabid animal. The subsequent genetic identification of the virus as a strain of rabies of bat origin provides some perspective on the mystery surrounding this case. Since 1980, seven of the nine cases of indigenously acquired rabies in humans in the United States have been associated with strains of rabies virus primarily found in bats, but only rarely identified from terrestrial mammals [1, 2]. Four of the seven individuals who subsequently died of rabies of bat origin reported no history of contact with any rabid animal. The silver-haired bat *Lasionycterus noctivagans* has been implicated as the primary reservoir of one strain of bat-associated rabies virus implicated in human deaths in several states [2–4]. Nucleic acid sequence analyses of these strains show almost total genetic homology with viral sequences obtained from the New York case [1].

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

Rabies in bats in the United States has been reported from all 48 contiguous states [2, 5], and during 1992 six states recorded rabies only in these volant mammals [6]. The total number of cases of rabies in bats reported to the Centers for Disease Control and Prevention (CDC) has increased dramatically since 1953 when rabies was discovered in insectivorous bats of the United States. In 1992, 647 cases were reported with California, Texas and New York recording the largest numbers (104, 69, 59 respectively) [6]. The annual CDC summary of rabies in wildlife does not identify the bats to species, as many state laboratories lack the resources to make such identifications. New York State, however, does identify bats to species and records information on all animals submitted for rabies testing. These data were used to examine the epidemiology of bat rabies in this state in detail.

MATERIALS AND METHODS

Bat submissions

Total annual numbers of rabid bats from New York were summarized from CDC records from the year when bat rabies was first reported in the state (1956) through 1992.

Detailed analyses were performed for specimens submitted from 1 January 1988 through 31 December 1992, a period when the New York State laboratory received more than 7000 bats or bat tissues for rabies testing. The majority of these animals were found by state residents in or around their homes and had not been involved in a biting incident. When bats were involved in biting or had other direct contact with humans or domestic animals (e.g. found within or near a house or killed by a pet), this information was noted on the specimen submission form. These data do not reflect a systematic study of the species composition of bats in New York State or the true prevalence of rabies in these species. Rather, they reflect the relative prevalence of various species and the frequency of their interaction with humans or their domestic pets.

When intact bats were submitted, these were identified to species and sex, and classified as adults or juveniles on the basis of size and colour of the pelage.

Rabies testing

Bats, or tissues from bats, were submitted for rabies testing to the New York State rabies laboratory for diagnosis. Brains were removed and all tissues were assessed as to their condition and appropriateness for detection of rabies viral antigens (i.e. suitable for testing, decomposed, mutilated, or inappropriate tissue). Smears of brain tissue were tested for rabies viral antigens by application of fluorescein isothiocyanate-conjugated antisera [7].

Data analysis

The data were analysed using SPSS [8] and Epi Info [9]. The statistical tests used and levels of significance are specified in the text. The actual number of rabid bats of each species was compared with an expected number, based on the respective contribution to each species to the total number of submitted bats. Bonferroni confidence intervals (95%) were used to generate estimates of the proportion (%) of rabies virus infection for each species [10]. In these analyses, an

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

upper standard normal table value corresponding to a probability tail of $\alpha/2k$ ($Z_{\alpha/2k}$) was selected for $\alpha = 0.05$ and $k = 7$ species of bats. In this case $Z_{\alpha/2k} = Z_{0.0036} = 2.69$.

RESULTS

Species tested and prevalence of rabies

The number of rabid bats reported from New York has increased from 1 in 1956 to a maximum of 84 in 1990 (Fig. 1).

During 1988–92, 7238 bats were received of which 7047 were identified as belonging to one of seven species: the big brown bat, *Eptesicus fuscus* (62%), the small brown bat (*Myotis lucifugus*, 31%), Keene's bat (*Myotis keenii*, 4·7%), the red bat (*Lasiurus borealis*, 1·2%), the hoary bat (*L. cinereus*, 0·6%), the silver-haired bat (*Lasionycterus noctivagans*, 0·4%), and the northern pipistrelle (*Pipistrellus subflavus*; 0·1%) (Table 1).

Of the 7238 bats submitted, 6810 were suitable for rabies testing and 312 (4·6%) were positive for rabies virus. Of these, 308 were identified to species and included 276 *E. fuscus* (90% of the total rabid bats; Table 2). At least two positive bats were found in each of the other six species tested over the 5-year period. The pooled rabies prevalence over the 5-year period for each species was, in descending order, *P. subflavus* (20%), *L. cinereus* (10%), *La. noctivagans* (8·0%), *E. fuscus* (6·3%), *L. borealis* (4·8%) and *M. lucifugus* (0·7%). The annual prevalence of rabies was stable for *E. fuscus*, the species best represented, varying from 5·9% in 1988 to 7·4% in 1990 ($\chi^2 = 1.64$; D.F. $= 4$; $P = 0.80$).

The number of specimens of each species positive for rabies virus was significantly different from the numbers expected based on the distribution of each species in the total bat population tested ($\chi^2 = 126$; D.F. $= 6$; $P < 0.001$). The Bonferroni intervals indicated that for three species the expected number of rabies cases predicted was significantly different from that observed. The number of *E. fuscus* found positive for virus was significantly higher than expected, while the numbers of *M. lucifigus* and *M. keenii* were significantly lower (Table 3). For all other species the prevalence did not differ significantly from that expected (Table 3).

Bat demographics and rabies

Rabid bats were found from almost every county in New York State from which specimens were submitted (Fig. 2). The prevalence of positive bats from counties in which at least one positive was found varied from 0·8–25·0%. When New York State was divided into eastern ($n = 27$ counties) and western counties ($n = 30$ counties), there was no significant difference in the prevalence of rabies (4·5% from both areas, slightly lower than the overall rabies prevalence of 4·6% for the state, as these data included a denominator [$n = 7160$ submissions] not adjusted for bats unsuitable for testing). In addition, there was no obvious pattern to the distribution of species among counties.

Of the 6810 bats tested for rabies virus, 49% were female and 51% were male. The overall prevalence of rabies was significantly higher among female (5·1%, $n = 166$ positive) than among male bats (3·9%, $n = 126$ positive; $\chi^2 = 7.69$; D.F. $=$ 1; $P = 0.006$). When individual species were considered, a significant difference was

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

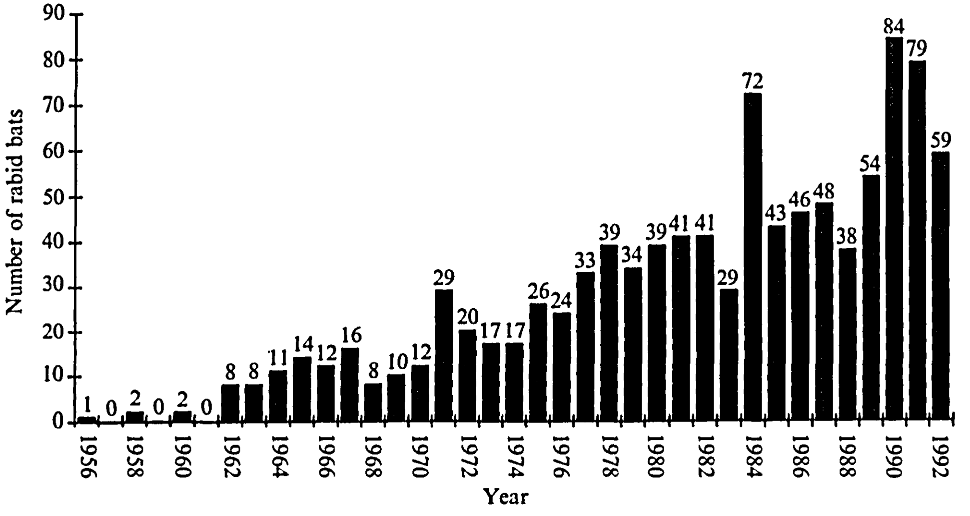

Fig. 1. Number of cases of bat rabies diagnosed in New York State from 1956–92.

detected only for *E. fuscus*, for which 8·7% ($n = 1737$) of female bats and 5·0% ($n = 2202$) of male bats were positive ($\chi^2 = 20·86$; D.F. = 1; $P < 0·001$).

Of the bats examined 6841 (94·5%) were classified as adult and 289 (4·0%) as juveniles with 108 (1·5%) being unclassified. The prevalence of rabies was significantly higher among adult bats (4·7% positive, $n = 6478$ tested) than among juvenile bats (1·8% positive, 275 tested; $\chi^2 = 5·11$; D.F. = 1; $P = 0·02$). *E. fuscus* again contributed most to this significant finding, as more adults were infected (6·9%, $n = 3929$ tested) than juveniles (2·5% infected, $n = 204$ tested; $\chi^2 = 6·15$; D.F. = 1; $P = 0·01$). None of the other species examined had sufficient numbers of individual bats classified by age and rabies virus status to make comparisons meaningful.

Reported bat bites, contacts and rabies

Of the 7047 bats identified to species, 832 (12%) had reported histories of a biting incident ($n = 303$; 36% of all contacts) or other contact ($n = 529$; 64% of all contacts) with humans or domestic pets. Overall, bats involved in a biting incident were significantly more likely to be rabid (8·1%, $n = 284$ bats, 19 were excluded as unsuitable for rabies testing) than were bats involved in other contacts (4·5% rabid, $n = 488$, 41 bats excluded; $\chi^2 = 4·22$; D.F. = 1; $P = 0·04$) or bats submitted for unknown reasons (4·4% positive, $n = 5916$, 298 bats excluded; $\chi^2 = 8·22$; D.F. = 1; $P = 0·004$).

The majority of the reported contacts involved *E. fuscus*, with 196 bats submitted following bites and an additional 317 submitted for other contacts. More *E. fuscus* submitted for bites were rabid (11%, excluding 11 bats involved in bites but unsuitable for testing) than were those submitted for other contacts (6·5% rabid, excluding 24 bats; $\chi^2 = 2·22$; D.F. = 1; $P = 0·14$, *ns*), or for unknown reasons (6·5%, $n = 3665$, excluding 174 bats; $\chi^2 = 4·03$, $P = 0·04$). A similar trend existed for *M. lucifugus*, with 2·4% of individuals submitted for bite being positive for rabies virus ($n = 82$, 7 bats involved in bites excluded) compared with only 0·7% ($n = 136$, 14 bats excluded) positive when submitted for other contacts and 0·7% positive when submitted for unknown causes ($n = 1852$, 113 bats excluded.

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

Table 1. *Numbers (% of annual total) and species composition of bats tested for rabies in New York State from 1988–92*

	Year					
	1988	1989	1990	1991	1992	Total
E. fuscus	640 (55·9)	783 (62·9)	1027 (59·8)	1073 (66·5)	830 (62·5)	4353 (61·8)
M. lucifugus	422 (36·9)	371 (29·8)	578 (33·7)	428 (26·5)	405 (30·5)	2204 (31·3)
M. keenii	61 (5·3)	59 (4·7)	79 (4·6)	70 (4·3)	64 (4·8)	333 (4·7)
L. borealis	13 (1·1)	18 (1·4)	13 (0·8)	27 (1·7)	12 (0·9)	83 (1·2)
L. cinereus	4 (0·3)	9 (0·7)	9 (0·5)	8 (0·5)	9 (0·7)	39 (0·6)
La. noctivagans	3 (0·3)	3 (0·2)	5 (0·3)	6 (0·4)	8 (0·6)	25 (0·4)
P. subflavus	1 (0·1)	1 (0·1)	6 (0·3)	2 (0·1)	0 (0·0)	10 (0·1)
Total	1144	1244	1717	1614	1328	7047

Table 2. *Numbers of confirmed cases of rabies in bats (% of annual rabies cases in bats) from New York State, 1988–92*

	Year						
	1988	1989	1990	1991	1992	*N* positive	Positive (%)*
E. fuscus	36 (97·3)	50 (92·6)	74 (88·1)	67 (85·9)	49 (89·1)	276 (89·6)	6·3
M. lucifugus	—	3	6	4	3	16 (5·2)	0·7
M. keenii	1	—	—	1	2	4 (1·2)	1·2
L. borealis	—	—	1	3	—	4 (1·2)	4·8
L. cinereus	—	—	1	2	1	4 (1·2)	10·3
La. noctivagans	—	1	—	1	—	2 (0·6)	8·0
P. subflavus	—	—	2	—	—	2 (0·6)	20·0
Total	37	54	84	78	55	308	4·4

* Overall prevalence of rabies by species pooled for 5 years calculated with total figures from Table 1.

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

Table 3. *Numbers of confirmed cases of rabies in bats from New York State, 1988–92*

Species	Observed N	Observed %	Expected N	Expected %	Bonferroni 95% confidence intervals
E. fuscus	276	89·6	190	61·8	85% ⩽ P ⩽ 94%*
M. lucifugus	18	5·2	96	30·5	1·8% ⩽ P ⩽ 8·6%†
M. keenii	4	1·3	15	4·7	0·0% ⩽ P ⩽ 3·0%†
L. borealis	4	1·3	4	1·2	0·0% ⩽ P ⩽ 3·0%
L. cinereus	4	1·3	2	0·6	0·0% ⩽ P ⩽ 3·0%
La. noctivagans	2	0·6	1	0·4	0·0% ⩽ P ⩽ 1·8%
P. subflavus	2	0·6	< 1	0·1	0·0% ⩽ P ⩽ 1·8%

* $P < 0·05$, observed greater than expected.
† $P < 0·05$, observed less than expected.

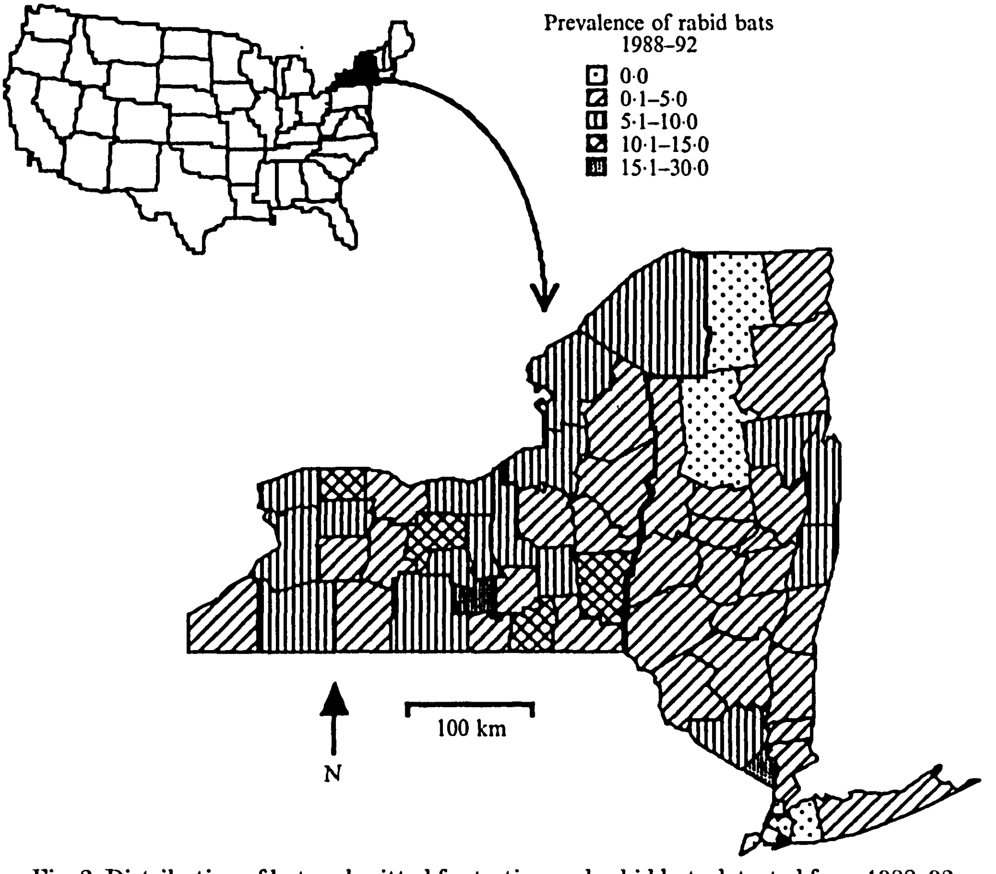

Fig. 2. Distribution of bats submitted for testing and rabid bats detected from 1988–92 for each county in New York. The bold line defines the eastern and western regions of the state described in the text.

However, none of the differences for *M. lucifugus* reached the 5% level of statistical significance. Summation of all other species resulted in a similar trend, with 12% ($n = 17$, 1 bat excluded) positive when submitted for bite compared with 3·4% ($n = 59$, 3 bats excluded) when submitted for other contacts or 3·0% for unknown cause ($n = 399$, 11 bats excluded).

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

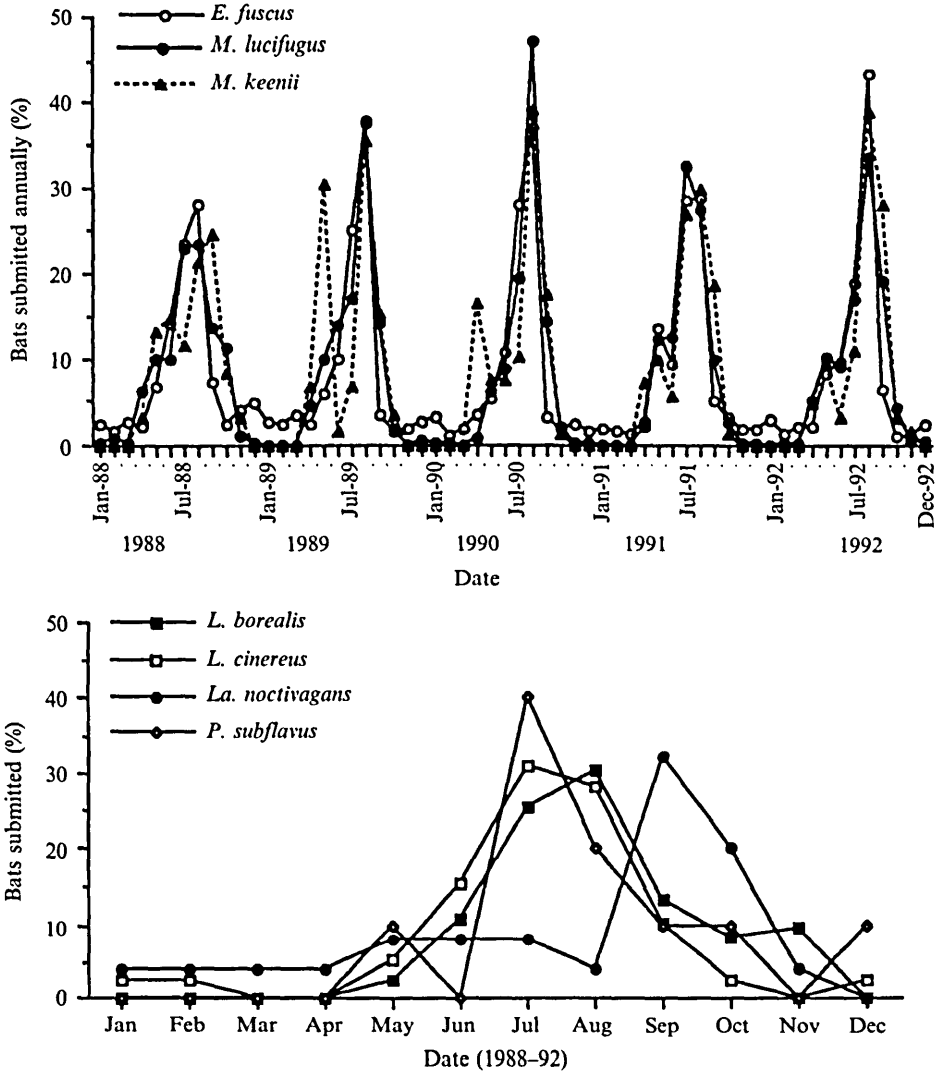

Fig. 3. Percentage of bat submissions by month for each year (1988–92) for bats tested for rabies. The three most common species (*Eptesicus fuscus*, *Myotis lucifugus*, and *M. keenii*) are shown in the upper panel. Percentage of submissions by month pooled for the period 1988–92 for four infrequently submitted bat species (*Lasiurus borealis*, *Lasiurus cinereus*, *Lasionycteris noctivagans* and *Pipistrellus subflavus*) are shown in the lower panel.

Seasonal trends

The majority of bats examined for rabies virus during 1988 to 1992 were submitted during the summer months, with 35% of the total submissions being in August (Fig. 3). *Eptesicus fuscus*, *M. lucifugus* and *M. keenii* showed characteristic seasonal peaks. There was a consistent bimodality in the submissions of *M. keenii*, with a minor peak in submissions in April or May. This peak was occasionally discernible for other species. A similar pattern, with a suggestion of bimodality, was also seen with *P. subflavus* when the annual samples were pooled.

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

Lasiurus borealis and *L. cinereus* showed similar patterns to the other Vespertilionids, while *La. noctivagans* submissions peaked later in the autumn (September), although total numbers were too small to allow statistical evaluations.

Of the 6688 bats submitted for rabies testing for which date and species information were available, 308 (4·6%) were positive. The monthly distribution of numbers of rabid bats was significantly different from what would be expected by chance based on the numbers of bats submitted for testing ($\chi^2 = 92$; D.F. = 11; $P < 0{\cdot}001$; Fig. 4). The expected proportion of rabid bats identified in September (8·6% of the 308 rabid bats identified) was significantly less than the proportion observed (19% of the total; Bonferroni 95% CI = 13–26%), as was also true for October (2·9% of total expected; 8·4% observed; Bonferroni 95% CI = 3·9–13%). Significantly fewer rabid bats were found in August (35% expected; 24% observed; Bonferroni 95% CI = 17–31%). All other months were within the expected range.

DISCUSSION

The occurrence of enzootic rabies in bats remains a public health problem, as evidenced by the recent rabies-related deaths in New York [1] and Texas [4]. Strains of rabies virus in bats have accounted for seven of the nine indigenously acquired human cases of rabies in the United States since 1980. The implication of *La. noctivagans* as the source of the virus in both these recent cases is noteworthy. Only rarely were *La. noctivagans* submitted for rabies testing in New York (25 bats) and only two were found positive during 1988–92. The rabies virus variant, as identified by monoclonal antibodies, most commonly found in this species (11 of 12 isolates), was only rarely present in other bat species (5 of 238 isolates) [1], but has been implicated in the deaths of 5 of the 7 persons who have died of infection with rabies virus variants associated with bats in the United States since 1980 [4].

This analysis is based on one of the largest series of bats to be examined for rabies virus from a single State [11–13]. That only 12% of the bats tested during the period 1988–92 had histories of contact or bite makes these data unusually useful for assessing trends. Most laboratories in the United States only test animals if either rabies is suspected, due to the display of unusual behaviour, or there is evidence of physical contact with a human or a domestic pet [6]. Although biases certainly exist in the submission of bats by the public, these data are probably more representative of the status of rabies virus infection in common species of bats.

The relative abundance of colonial species submitted (*E. fuscus*, *M. lucifugus*, *M. keenii* and *P. subflavus*; 97% of total submissions) compared with solitary species (*L. borealis*, *L. cinereus* and *La. noctivagans*; 3% of submissions) probably reflects both the abundance of different species and their likelihood of interacting with humans. These factors certainly contributed to the numerical dominance of *E. fuscus* (62% of the total submissions) and its contribution to the total number of rabies virus infected bats detected (90%). In contrast, in a review of nationally reported bat rabies from 1953–65 [12], only 59% of the rabid bats were colonial species with *E. fuscus* accounting for 17%.

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

Of the different bat species tested in the United States [11, 14–17] and Canada [18, 19], the species of bats exhibiting solitary lifestyles typically have the highest prevalences of rabies, with as many as 25% of individuals being positive, with less than 1% of the members of colonial species being positive [20]. In contrast, our survey found rabies virus infection was most prevalent among a colonial species, *P. subflavus* (20% positive), but only 10 individuals were submitted. For the other colonial species, the prevalence of rabies for *E. fuscus* (6%) exceeded that for *M. lucifugus* (1%), which is the typical [17, 18, 21–23], but not universal pattern [11]. The prevalence of rabies in solitary species from New York varied from 5–10%, well within the range reported for colonial species from this state. However, solitary living species contributed only 3·2% of the 308 cases of rabies diagnosed in bats during this 5-year period.

The higher prevalence of rabies in solitary bats noted in previous reports, is unexpected since the social behaviour of colonial species should provide greater opportunities for transmission of an infectious agent. Explanations for previous findings include the aggressive nature of rabid solitary bats [19, 24], the precipitation of clinical rabies by the stress of migration [11], or the variation in the susceptibility of different bat species to rabies infection with strains of rabies virus which vary among bat species [3, 25]. Our results indicate that rabies in colonial species in New York is within a range similar to that of solitary species and occurs more frequently in some species (*E. fuscus*) than was expected (Table 3).

The overall prevalence of rabies among bats from our study (5%) was higher than the 2% (based on viral isolation or FAT) found in a previous study of *E. fuscus* (3% positive) and *M. lucifugus* (< 1% positive) captured from wild colonies in New York State [22]. A similar study of presumably healthy bats in Massachusetts found 5 of 490 bats to be infected with rabies virus compared to 3 of 30 bats submitted by citizens [21]. In Massachusetts rabies infection was found in < 1% of *M. lucifugus* and in 4% of *E. fuscus*.

Our observation of a significantly higher prevalence of rabies among female *E. fuscus* was unexpected since most studies show a similar prevalence in each sex [14, 18, 23], although in Illinois a female sex bias in rabies prevalence was apparent when results from all bat species were pooled [11]. The higher prevalence of rabies in female bats and the finding that adult *E. fuscus* are more commonly infected than are juveniles (7% of adults compared with 3% of juveniles) may be linked. Adult female *E. fuscus* form nursery colonies in houses and outbuildings and may be more frequently collected and submitted for testing. As rabies in bats is probably acquired by horizontal transmission [26], older animals have a greater cumulative risk of infection. The proximity of humans to bats in nursing colonies may provide those extra female bats that skew the sex ratio of rabies infected bats. Adult male *E. fuscus* may join nursery colonies in late summer, although an extensive survey in Ohio found they never constituted more than 10% of those groups [27].

The overall seasonal pattern of bat submissions and prevalence of rabies in New York was similar to that reported from other states and Canada, with a late summer or early autumn peak [11, 13, 17, 18, 28]. The submission pattern presumably reflects both increased bat activity and their presence in houses

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

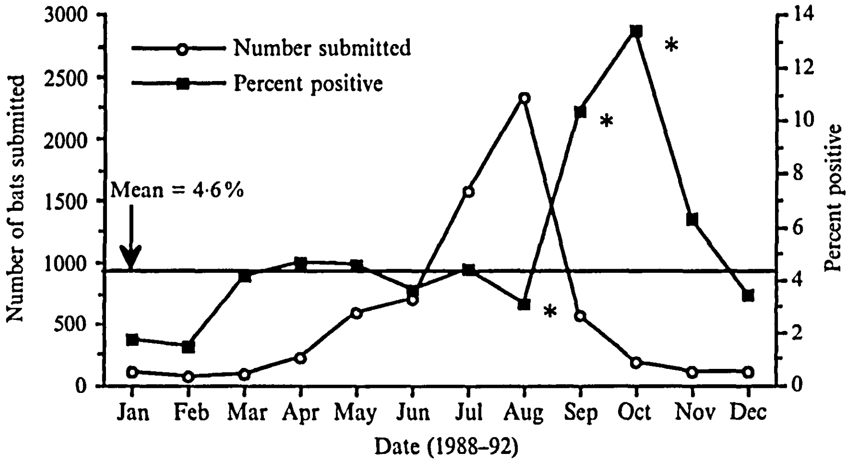

Fig. 4. Number of total bat submissions by month pooled for the period 1988–92 and percentage of bats positive for rabies. The * indicates months with significantly ($P < 0·05$) fewer positive bats detected (August) or significantly more positive bats detected (September and October) than expected.

during summer months, and the birth of young in June and July [27]. The significant dip in the prevalence of infection in submitted bats in New York during August (Fig. 3) may be related to the presence of subadult animals which have not yet been exposed to rabies or are in an early incubation phase. The subsequent peak in rabies during the autumn presumably reflects the transmission of virus which occurred in nursery colonies earlier in the summer and the lag associated with the incubation period. Rabies virus infection can be acquired by young bats soon after birth in some colonial species, such as *Tadarida brasiliensis* [26]. Factors such as migratory stress may also explain in part the increase in rabies cases in September and October (Fig. 4).

Few public health measures are available that would reduce the rare transmission of bat-associated strains of rabies virus to humans. Education efforts aimed at warning the public about the dangers of handling bats may reduce the number of human rabies cases by a few, but most of the recent victims of bat-associated rabies have no memory of receiving a bite or any other contact with a bat. Other activities, such as the intentional establishment of bat roosts around homes, should not be encouraged. As a prudent safety precaution, persons should seek rabies post-exposure treatment following any physical contact with a bat especially when a bite or mucous membrane contact cannot be excluded.

REFERENCES

1. Human rabies – New York, 1993. MMWR 1993; **42**: 799–806.
2. Baer GM, Smith JS. Rabies in nonhematophagous bats. In: Baer GM, ed. The natural history of rabies. Boca Raton: CRC Press, 1991: 341–66.
3. Smith JS. Monoclonal antibody studies of rabies in insectivorous bats of the United States. Rev Infect Dis 1988; **10 Suppl 4**: S637–43.
4. Human rabies, 1993 – Texas and California. MMWR 1994; **43**: 93–6.
5. Constantine DG. An updated list of rabies-infected bats in North America. J Wildl Dis 1979; **15**: 347–9.

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press

6. Krebs JW, Strine TW, Childs JE. Rabies surveillance in the United States during 1992. J Am Vet Med Assoc 1993; **203**: 1718–31.
7. Trimarchi CV, Debbie JG. The fluorescent antibody in rabies. In: Baer GM, ed. The natural history of rabies. Boca Raton: CRC Press, 1991: 219–33.
8. Norusis MJ. SPSS for Windows 6.0. Chicago: SPSS Inc., 1993.
9. Dean AG, Dean JA, Burton AH, Dicker RC. Epi Info, Version 5: a word processing, database, and statistics program for epidemiology on microcomputers. Atlanta: Centers for Disease Control, 1990.
10. Byers CR, Steinhorst RK, Krausman PR. Clarification of a technique for analysis of utilization-availability data. J Wildl Manage 1984; **48**: 1050–3.
11. Burnett CD. Bat rabies in Illinois: 1965 to 1986. J Wildl Dis 1989; **25**: 10–19.
12. Baer GM, Adams DB. Rabies in insectivorous bats in the United States, 1953–65. Public Health Rep 1970; **85**: 637–45.
13. Constantine DG. Bat rabies in the southwestern United States. Public Health Rep 1967; **82**: 867–88.
14. Bigler WJ, Hoff GL, Buff EE. Chiropteran rabies in Florida: a twenty-year analysis, 1954 to 1973. Am J Trop Med Hyg 1975; **24**: 347–52.
15. Whitaker JO, Miller WA. Rabies in bats of Indiana: 1968–1972. Proc Ind Acad Sci 1974; **83**: 469–72.
16. Schneider NJ, Scatterday JE, Lewis AL, Jennings WL, Venters HD, Hardy AV. Rabies in bats in Florida. Am J Public Health 1957; **47**: 983–9.
17. Kurta A. Bat rabies in Michigan. Pap Mich Acad Sci Arts Let 1979; **12**: 221–30.
18. Pybus MJ. Rabies in insectivorous bats of western Canada, 1979 to 1983. J Wildl Dis 1986; **22**: 307–13.
19. Schowalter DB. Characteristics of bat rabies in Alberta. Can J Comp Med 1980; **44**: 70–6.
20. Baer GM. Rabies in nonhematophagous bats. In: Baer GM, ed. The natural history of rabies. New York: Academic Press, 1975: 79–97.
21. Girard KF, Hitchcock HB, Edsall G, MacCready RA. Rabies in bats in southern New England. N Engl J Med 1965; **272**: 75–80.
22. Trimarchi CV, Debbie JG. Naturally occurring rabies virus and neutralizing antibody in two species of insectivorous bats of New York State. J Wildl Dis 1977; **13**: 366–9.
23. Steece RS, Erickson TJ, Siem RA. Chiropteran rabies in Minnesota: 1976–1980. J Wildl Dis 1982; **18**: 487–9.
24. Bell GP. A possible case of interspecific transmission of rabies in insectivorous bats. J. Mammal 1980; **61**: 528–30.
25. Smith JS. Rabies virus epitopic variation: use in ecologic studies. Adv Virus Res 1989; **36**: 215–53.
26. Constantine DG. Absence of prenatal infection of bats with rabies virus. J Wildl Dis 1986; **22**: 249–50.
27. Mills RS, Barrett GW, Farrell MP. Population dynamics of the big brown bat (*Eptesicus fuscus*) in southwestern Ohio. J Mammal 1975; **56**: 591–604.
28. Pool GE, Hacker CS. Geographic and seasonal distribution of rabies in skunks, foxes and bats in Texas. J Wildl Dis 1982; **18**: 405–18.

https://doi.org/10.1017/S0950268800068515 Published online by Cambridge University Press