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# BAT RABIES IN ILLINOIS: 1965 TO 1986 

## Christopher D. Burnett

Section of Wildlife Research, Illinois Natural History Survey, 607 East Peabody Drive, Champaign, Illinois 61820, USA
abstract: From 1968 to 1986, Illinois (USA) citizens and agencies submitted 4,272 bats to the Illinois Department of Public Health for rabies testing. Of this number, $6 \%$ tested positive, a rate comparable to similar studies from other parts of North America. Due to sampling biases, the true infection rate among bats in Illinois is probably lower than $6 \%$. Additional analysis relied on a subsample ( $n=2,433$ ) of the specimens collected from 1965 to 1986 . Prevalences were significantly different among years, but no linear trends were found over the study period. Evidence for a local outbreak of bat rabies was found. Prevalences for the species with sample sizes adequate for statistical analysis were, from high to low: hoary bat (Lasiurus cinereus), $11 \%$; red bat (L. borealis), $5 \%$; silver-haired bat (Lasionycteris noctivagans), 4\%; little brown bat (Myotis lucifugus), 4\%; big brown bat (Eptesicus fuscus), 3\%; Keen's bat (Myotis keenii), 2\%; and evening bat (Nycticeius humeralis), $2 \%$. The higher prevalences found among the non-colonial species (hoary, red and silver-haired bats) were consistent with similar studies. Considerable annual variation in prevalences was found within species, and the prevalence rankings of the species varied over the study period. Prevalences were significantly higher in females ( $6 \%$ ) than in males ( $4 \%$ ) when species were pooled, but no significant differences between sexes were found within species. In contrast to the other species analyzed, all of which had sex ratios favoring females, the big brown bat sample had a large majority of males. Prevalences were significantly higher in adults (6\%) than in juveniles (3\%) when species were pooled. Within individual species, significant differences between age groups were found only for hoary and red bats; in two species, juveniles had higher prevalences. Above average prevalences were observed in May and August to November. Southern Illinois had the highest prevalences; prevalences were intermediate in the north and lowest in the central region. Overall, the patterns of rabies prevalence among bats submitted by the public in Illinois from 1965 to 1986 were similar to those reported from other parts of North America.

Key words: Rabies prevalence, bats, Illinois, interspecific, sex, age, geography.

## INTRODUCTION

Although the transmission of bat rabies to humans is rare (Tuttle and Kern, 1981), sensational journalism has caused many in the United States to think of bats as a serious threat to health. Consequently, state testing laboratories receive many bat specimens from concerned citizens, local agencies and veterinarians. Although these specimens do not constitute an unbiased sample of wild populations, they can provide useful information about the prevalence of rabies in bats if the data are carefully interpreted.

In this study, 22 yr ( 1965 to 1986) of data from bats submitted for rabies testing by Illinois citizens and local agencies are analyzed. The prevalence of rabies by species, sex and age are compared and longterm, seasonal and geographic trends are examined. Results are discussed in relation to biological factors and sampling biases associated with publicly submitted bats.

## MATERIALS AND METHODS

Two overlapping data sets were used. One was obtained from the records of the Illinois Department of Public Health (Division of Infectious Diseases, 535 West Jefferson Street, Springfield, Illinois 62761, USA) (IDPH) and consists of the number of bats tested and the number that tested positive during the 18 yr period, 1969 to 1986. These data include the results of all testing by IDPH and the Illinois Department of Agriculture (Division of Meat, Poultry and Livestock Inspection, Springfield, Illinois 62706, USA). Data on the number of bats that tested positive were also obtained from IDPH for the years 1959 to 1968, but records were not kept on the number tested during those years. Since the early 1960's, these Illinois laboratories used the fluorescent antibody method (Kissling, 1975) for diagnosing rabies.
The second data set was derived from already tested specimens sent by the testing laboratories to the Illinois Natural History Survey (Section of Wildlife Research, 607 East Peabody Drive, Champaign, Illinois 61820, USA) (INHS) over the 22 yr period, 1965 to 1986. Thus, with the exception of 1965 to 1968, the INHS sample is a subset of the IDPH sample. The smaller sam-


Figure 1. Annual sample sizes of bats tested for rabies in Illinois (1969 to 1986) and sample sizes of the subset processed by the Illinois Natural History Survey (1965 to 1986).
ple was used because the IDPH data did not include information on species, age, sex, or collection locality. Initially, I assumed that the INHS specimens were a random sample of all the bats tested. Species identifications were made by G. C. Sanderson (1965 to 1980), C. D. Burnett (1981 to 1986) and J. E. Gardner (1984 to 1986). Age was determined by the appearance of the metacarpal epiphyses (Kunz and Anthony, 1982). Locality data were obtained from sheets shipped with the specimens. The specimens are preserved in alcohol and maintained in the mammalogy collections at the University of Illinois (Museum of Natural History, 1301 West Green Street, Urbana, Illinois 61801, USA) or at the INHS.

For some comparisons, I divided the species examined into two ecologically similar groups, colonial bats and non-colonial bats. The species included in the colonial group were: little brown bat (Myotis lucifugus), Keen's myotis (M. keenii), Indiana bat (M. sodalis), eastern pipistrelle (Pipistrellus subflavus), big brown bat (Eptesicus fuscus) and evening bat (Nycticeius humeralis). These species generally rear their young in groups and do not migrate long distances. The species included in the non-colonial group were: silver-haired bat (Lasionycteris noctivagans), red bat (Lasiurus borealis) and hoary bat (L. cinereus). These species generally rear their young solitarily and migrate long distances.

An ARC/INFO geographic information system (ESRI, 1987) was used for data management and to generate maps showing geographic patterns. Chi-square analysis was used to test for differences in rabies prevalence by species, sex, age, year, month and geographic region, and for deviations from expected sex ratios within species. For regional comparisons, I divided the


Figure 2. Annual rabies prevalences of bats tested in Illinois (1969 to 1986) and for the bats processed by the Illinois Natural History Survey (1965 to 1986).
state into three arbitrary sections after Graber and Graber (1976). Simple linear regression was used to test for trends in rabies prevalences over the study period.

## RESULTS

## Overall prevalence of rabies

Over the study period, the number of bats submitted to IDPH for testing increased, but this trend has reversed in recent years (Fig. 1). Based on the IDPH data set ( $n=4,272$ ), the overall prevalence of rabies in bats submitted for testing in Illinois for the 18 yr period, 1969 to 1986, was $6 \%$ with a range from $2 \%$ (1969 and 1970) to $11 \%$ (1983) (Fig. 2). Although the prevalences obtained from the INHS subsample for the same period had a wider variance among years, the overall INHS prevalence was also $6 \%$ and the annual variations generally followed the pattern of the IDPH data (Fig. 2). For the full 22 yr period, which included relatively low prevalences for 1965 to 1968, the INHS data yielded an overall rabies prevalence of $5 \%$ (Table 1 ).

## Species, sex and age differences

Seven of the nine identified species of bats had sample sizes large enough for statistical analysis (Table 1). Rabies prevalences ranged from a high of $11 \%$ in hoary bats to a low of $2 \%$ in evening bats. The non-colonial species had higher prevalences than the colonial species. Variation

Table 1. Percentages of bats publicly submitted in Illinois (1965 to 1986) that tested positive for rabies by species, sex and age. Species are listed in order of overall prevalence of rabies.

| Species | Sex |  | Age |  | Total- |
| :---: | :---: | :---: | :---: | :---: | :---: |
|  | Males | Females | Adults | Juveniles |  |
| Hoary bat | $\begin{gathered} 8 \mathrm{NS} \\ (86)^{\mathrm{b} * * *} \end{gathered}$ | $\begin{gathered} 13 \\ (175) \end{gathered}$ | $\begin{gathered} 16^{* * *} \\ (168) \text { NT } \end{gathered}$ | $\begin{gathered} 2 \\ (92) \end{gathered}$ | $\begin{gathered} 11 \\ (270) \end{gathered}$ |
| Red bat | $\begin{gathered} 5 \mathrm{NS} \\ (352)^{* *} \end{gathered}$ | $\begin{gathered} 6 \\ (441) \end{gathered}$ | $\begin{gathered} 7^{* * *} \\ (532) \text { NT } \end{gathered}$ | $\begin{gathered} 2 \\ (214) \end{gathered}$ | $\begin{gathered} 5 \\ (830) \end{gathered}$ |
| Silver-haired bat | $\begin{gathered} 5 \mathrm{NS} \\ (79)^{* * *} \end{gathered}$ | $\begin{gathered} 3 \\ (131) \end{gathered}$ | $\begin{gathered} 4 \mathrm{NT} \\ (188) \mathrm{NT} \end{gathered}$ | $\begin{gathered} 0 \\ (4) \end{gathered}$ | $\begin{gathered} 4 \\ (216) \end{gathered}$ |
| Little brown bat | $\begin{gathered} 4 \mathrm{NS} \\ \text { (48) NS } \end{gathered}$ | $\begin{gathered} 4 \\ (56) \end{gathered}$ | $\begin{gathered} 3 \mathrm{NT} \\ (90) \mathrm{NT} \end{gathered}$ | $\begin{gathered} 9 \\ (11) \end{gathered}$ | $\begin{gathered} 4 \\ (107) \end{gathered}$ |
| Big brown bat | $\begin{array}{r} 3 \mathrm{NS} \\ (528)^{* * *} \end{array}$ | $\begin{gathered} 5 \\ (314) \end{gathered}$ | $\begin{gathered} 3 \mathrm{NS} \\ (725) \mathrm{NT} \end{gathered}$ | $\begin{gathered} 4 \\ (96) \end{gathered}$ | $\begin{gathered} 3 \\ (878) \end{gathered}$ |
| Keen's myotis | $\begin{gathered} 6 \mathrm{NS} \\ (18)^{* *} \end{gathered}$ | $\begin{gathered} \mathbf{0} \\ (37) \end{gathered}$ | $\begin{gathered} 2 \mathrm{NT} \\ (52) \mathrm{NT} \end{gathered}$ | $\begin{gathered} 0 \\ (1) \end{gathered}$ | $\begin{gathered} 2 \\ (56) \end{gathered}$ |
| Evening bat | $\begin{gathered} 0 \mathrm{NS} \\ \text { (22) NS } \end{gathered}$ | $\begin{gathered} 3 \\ (35) \end{gathered}$ | $\begin{gathered} 2 \mathrm{NT} \\ (52) \mathrm{NT} \end{gathered}$ | $\begin{gathered} 0 \\ (4) \end{gathered}$ | $\begin{gathered} 2 \\ (60) \end{gathered}$ |
| All species | $\begin{gathered} 4^{*} \\ (1,138) \end{gathered}$ | $\begin{gathered} 6 \\ (1,200) \end{gathered}$ | $\begin{gathered} 6^{* * *} \\ (1,822) \text { NT } \end{gathered}$ | $\begin{gathered} 3 \\ (423) \end{gathered}$ | $\begin{array}{r} 5 \\ (2,433) \end{array}$ |

- Includes specimens of undetermined sex and age.
${ }^{\text {b }}$ Sample size.
- Includes six Indiana bats and 10 eastern pipistrelles.

NS, not significant ( $P \geq 0.05$ ); ${ }^{*} P<0.05$; $^{* *} P<0.01 ;{ }^{* * *} P<0.001$; NT, not tested.
in prevalences among species was highly significant ( $\chi^{2}=30.32$; df $=6 ; P<0.001$ ), and hoary and big brown bats contributed most to this variation.

For the combined species, the observed sex ratio was not significantly different from 1:1, but sex ratios were significantly biased in favor of females in four of the seven species (Table 1). Only the big brown bat sample had more males (63\%) than females (37\%).

Rabies prevalences were higher among females in four of seven species and in the pooled species, but this difference was significant only for the pooled species ( $\chi^{2}=$ 5.64; df $=1 ; P<0.025$ ) (Table 1). Big brown bats, with rabies prevalences of $5 \%$ in females and $3 \%$ in males had the statistically most significant differences between the sexes $\left(\chi^{2}=3.42 ; \mathrm{df}=1 ; P<\right.$ 0.10 ) of the seven species.

Sample sizes adequate for comparison between age classes were available only for hoary, red and big brown bats (Table 1). Among these three species, adults in the
two non-colonial species (hoary and red) had significantly higher rabies prevalences than did juveniles: $16 \%$ of the adult hoary bats compared to $2 \%$ of the juveniles ( $\chi^{2}$ $=34.58 ; \mathrm{df}=1 ; P<0.001$ ) and $7 \%$ of the adult red bats compared to $2 \%$ of the juveniles ( $\chi^{2}=8.53 ; \mathrm{df}=1 ; P<0.005$ ). Conversely, juveniles of the colonial big brown bat, had higher prevalences than did adults, but the difference was not significant. For all species combined, adults had significantly higher prevalences than did juveniles $\left(\chi^{2}=397.50 ; \mathrm{df}=1 ; P<\right.$ 0.001 ).

## Long-term trends

In 1959, Illinois became the twenty-third state to report rabies in bats when one publicly submitted specimen from Cook County and another from Macon County proved positive (Verts and Barr, 1961). From 1960 to 1964, another seven publicly submitted bats tested positive in Illinois, but data are not available to calculate prevalences of rabies infection before 1965 .

Table 2. Percentages of bats publicly submitted in Illinois (1965 to 1986) that tested positive for rabies by species and year. See text for species included in the colonial and non-colonial groups.

|  | Species |  |  |  |  |  |
| :---: | :---: | :---: | :---: | :---: | :---: | :---: |
| Year | Red | Hoary | Silver-haired | Non-colonial | Big brown | Colonial |
| 1965 | $0(41)^{2}$ | $18(11)$ | $5(20)$ | $4(72)$ | $3(29)$ | $3(38)$ |
| 1966 | $1(101)$ | $11(18)$ | $0(14)$ | $2(133)$ | $4(51)$ | $3(59)$ |
| 1967 | $2(42)$ | $0(12)$ | $0(5)$ | $2(59)$ | $0(37)$ | $0(44)$ |
| 1968 | $6(17)$ | $0(12)$ | $0(4)$ | $3(33)$ | $0(27)$ | $0(33)$ |
| 1969 | $0(26)$ | $0(2)$ | $33(3)$ | $3(31)$ | $0(5)$ | $0(10)$ |
| 1970 | $5(19)$ | $0(6)$ | $0(2)$ | $4(27)$ | $0(7)$ | $0(9)$ |
| 1971 | $24(21)$ | $50(4)$ | $0(2)$ | $26(27)$ | $0(9)$ | $0(16)$ |
| 1972 | $0(28)$ | $0(5)$ | $0(11)$ | $0(44)$ | $0(15)$ | $0(24)$ |
| 1973 | $6(17)$ | $9(11)$ | $0(4)$ | $6(32)$ | $0(17)$ | $4(23)$ |
| 1974 | $8(74)$ | $15(34)$ | $0(14)$ | $9(122)$ | $11(46)$ | $9(59)$ |
| 1975 | $5(43)$ | $0(17)$ | $0(21)$ | $3(81)$ | $2(42)$ | $2(61)$ |
| 1976 | $3(33)$ | $13(23)$ | $0(13)$ | $6(69)$ | $0(42)$ | $0(60)$ |
| 1977 | $2(43)$ | $8(24)$ | $10(10)$ | $5(77)$ | $0(39)$ | $0(51)$ |
| 1978 | $2(47)$ | $0(14)$ | $13(8)$ | $3(69)$ | $4(51)$ | $7(61)$ |
| 1979 | $4(27)$ | $0(18)$ | $0(6)$ | $2(51)$ | $0(31)$ | $0(37)$ |
| 1980 | $4(24)$ | $0(4)$ | $0(1)$ | $3(29)$ | $0(21)$ | $0(30)$ |
| 1981 | $5(20)$ | $0(2)$ | $0(3)$ | $4(25)$ | $0(21)$ | $0(24)$ |
| 1982 | $29(35)$ | $0(1)$ | $33(3)$ | $28(39)$ | $2(43)$ | $3(61)$ |
| 1983 | $10(62)$ | $19(16)$ | $4(23)$ | $10(101)$ | $11(94)$ | $10(122)$ |
| 1984 | $3(37)$ | $33(12)$ | $0(23)$ | $7(72)$ | $2(93)$ | $2(107)$ |
| 1985 | $5(43)$ | $31(16)$ | $9(23)$ | $11(82)$ | $5(86)$ | $5(105)$ |
| 1986 | $0(30)$ | $13(8)$ | $0(3)$ | $2(41)$ | $3(72)$ | $2(83)$ |

- Sample size.

From 1965 to 1986, trends in the prevalences of rabies infection for IDPH specimens were erratic (Fig. 2). Differences in prevalences among years for all species combined were highly significant ( $\chi^{2}=$ $64.30 ; \mathrm{df}=21 ; P<0.001$ ), but regression analysis showed no significant linear relationship between the percentage of bats that tested positive for rabies and the year in which the bats were tested. Rabies prevalences among INHS specimens, although generally lower, closely paralleled those of the IDPH specimens, with the exception of 1971 (Fig. 2).

Table 2 presents annual rabies prevalences for the four species that averaged $\geq 10$ specimens $/ \mathrm{yr}$ and for the colonial and non-colonial species groups. None of these species or groups exhibited significant linear trends in rabies prevalence over the study period. Prevalences within species varied widely among years, and relative prevalence rankings among species were not stable over time.

## Seasonal trends

Seasonal trends in bat submissions and rabies prevalences for the INHS specimens are presented in Figure 3. Submissions increased regularly from the beginning of the active season in March, peaked in August and then decreased until spring except for a minor peak in January. Rabies prevalences increased through spring, fell sharply during early summer, rose to a sustained peak in fall and then decreased through winter. The monthly prevalence of rabies was above average in May and August to November, and the differences in rabies prevalences among months were highly significant ( $\chi^{2}=29.69$; $\mathrm{df}=11 ; P$ $<0.005$ ). During the 22 yr study, no INHS specimens collected in February or March tested positive for rabies.
Table 3 gives the monthly prevalence and sample size data for the most commonly submitted species and for the two species groups. With minor variations, all


Figure 3. Monthly rabies prevalences and associated sample sizes for bat specimens (species combined) processed by the Illinois Natural History Survey (1965 to 1986). Horizontal line indicates overall prevalence (5\%) for these data.
of these species and groups followed the seasonal pattern of rabies prevalence shown in Figure 3.

## Geographic patterns

INHS specimens were collected in 73 of the 102 counties in Illinois, with a mean of 32 specimens per county ( $\mathrm{SD}=102$ ) (Fig. 4). In the northern region, specimens were collected primarily near Chicago ( $n$
$=839$ ) and Rockford ( $n=83$ ); in the central region, most specimens originated near Quincy ( $n=146$ ), Springfield ( $n=93$ ), and Danville ( $n=71$ ); the Carbondale area ( $n=160$ ) was the major source of specimens in the southern region. Cook County (Chicago area) accounted for $35 \%$ of the total INHS sample and also provided disproportionately large percentages of the specimens for the three non-colonial species ( $43 \%$ of the red bats, $53 \%$ of the hoary bats, and $60 \%$ of the silver-haired bats), and disproportionately small percentages of the colonial species.

The geographic pattern of rabies prevalences is presented in Figure 5. Twentyseven counties were represented by $\geq 10$ bats and the overall prevalences for those counties are shown on the map as integer percentages. Of the 46 counties represented by $<10$ bats, seven had $\geq 1$ rabiespositive specimen (dark shading) and 39 had no rabies-positive specimens (light shading). Twenty-nine counties (unshaded) were not represented in the INHS data. Rabies prevalences were highest in the south ( $15 \%, n=238$ ), lowest in the central region $(3 \%, n=537)$, and intermediate in the north ( $4 \%, n=1,408$ ). These differences were highly significant ( $\chi^{2}=64.26$; $\mathrm{df}=2 ; P<0.001$ ).

Table 3. Percentage of bats publicly submitted in Illinois (1965 to 1986) that tested positive for rabies by species and month. See text for species included in the colonial and non-colonial groups.

|  | Species |  |  |  |  |  |
| :--- | :---: | :---: | :---: | :---: | :---: | :--- |
| Month | Red | Hoary | Silver-haired | Non-colonial | Big brown | Colonial |
| Jan | $0(29)^{*}$ | $0(2)$ | $3(38)$ | $1(69)$ | $5(39)$ | $6(54)$ |
| Feb | $0(1)$ | $0(0)$ | $0(3)$ | $0(4)$ | $0(28)$ | $0(29)$ |
| M•r | $0(1)$ | $0(0)$ | $0(6)$ | $0(7)$ | $0(32)$ | $0(35)$ |
| Apr | $5(20)$ | $20(5)$ | $0(9)$ | $6(34)$ | $2(58)$ | $1(72)$ |
| May | $8(36)$ | $13(23)$ | $0(38)$ | $6(97)$ | $7(68)$ | $6(95)$ |
| Jun | $1(121)$ | $6(100)$ | $0(8)$ | $3(229)$ | $6(90)$ | $5(110)$ |
| Jul | $3(225)$ | $0(64)$ | $0(3)$ | $2(292)$ | $3(88)$ | $3(116)$ |
| Aug | $9(172)$ | $12(33)$ | $0(12)$ | $9(217)$ | $3(302)$ | $2(376)$ |
| Sep | $10(173)$ | $41(29)$ | $4(49)$ | $12(251)$ | $1(79)$ | $2(105)$ |
| Oct | $0(32)$ | $36(11)$ | $3(29)$ | $7(72)$ | $10(20)$ | $9(35)$ |
| Nov | $0(4)$ | $0(0)$ | $18(11)$ | $13(15)$ | $7(29)$ | $6(33)$ |
| Dec | $0(0)$ | $0(0)$ | $20(5)$ | $20(5)$ | $3(37)$ | $2(43)$ |

- Sample size


Figure 4. Numbers of bat specimens (species combined) processed by the Illinois Natural History Survey (1965 to 1986) by county. Heavy horizontal lines delineate regions of the state.

## DISCUSSION

## Overall prevalence of rabies

The overall prevalence figure of $6 \%$ obtained from the IDPH data (1969 to 1986) was based on the largest sample size and should be used for comparison with other studies. This figure proved comparable to prevalences reported in similar studies from other parts of North America: 7\% in Georgia, 1956 to 1965 (Richardson et al., 1966); 11\% in Kansas, 1966 (Birney and Rising, 1967); 5\% in Indiana, 1965 to 1972 (Whitaker and Miller, 1974); $4 \%$ in New York, 1972 to 1976 (Trimarchi and Deb-


Figure 5. Rabies prevalences by county for bat specimens (species combined) processed by the Illinois Natural History Survey (1965 to 1986). Heavy lines delineate regions of the state. Integer values are percentages of bats that tested positive for rabies in counties represented by $\geq 10$ bats (see Fig. 4). Dark shading indicates counties represented by $<10$ bats with one or more positive specimens. Light shading indicates counties represented by $<10$ bats with no positive specimens. Blank counties were not represented.
bie, 1977); 5\% in Michigan, 1965 to 1978 (Kurta, 1979); 5\% in Alberta, 1973 to 1978 (Schowalter, 1980); 3\% in Minnesota, 1976 to 1980 (Steece et al., 1982); $5 \%$ in western Canada, 1979 to 1983 (Pybus, 1986).

Although the prevalences for publicly submitted bats reported here and elsewhere accurately reflect the prevalence of rabies among bats captured by the public, they may not represent true infection rates
among bats in general or even among bats that are closely associated with people. Because healthy bats are generally difficult to capture and rabid bats frequently exhibit paralysis (Constantine, 1970), bats that roost in exposed locations are more likely to be captured and submitted for testing if they are rabid. Positive test results are also likely to stimulate increased concern about human exposure, thereby generating additional submissions from the same area (Whitaker and Miller, 1974). Thus, if local outbreaks of bat rabies occur, sampling bias may exaggerate general rabies prevalences.

Studies that have attempted to randomly sample clinically normal bats from the wild have reported rabies point prevalences of $0 \%$ to $3 \%$ (Girard et al., 1965; Constantine, 1967; Trimarchi and Debbie, 1977). Other studies indicate that prevalences in randomly selected bats are usually $<0.1 \%$ (Tuttle and Kern, 1981; Pybus, 1986). In Illinois, 652 bats collected from the wild in 1957 to 1958 showed no evidence of rabies based on the mouse inoculation method (Verts and Barr, 1961; Pearson and Barr, 1962). However, because bats infected with rabies are often paralyzed during the period that rabies can be demonstrated by laboratory tests, "random" surveys based on bats captured in flight may underestimate prevalences. Studies that rely on specimens captured in roosts are also likely to underestimate prevalences if the bats roost in inaccessible crevices. Conversely, if bats roost in exposed locations, sick bats will be more likely captured and prevalences will tend to be overestimated. Thus, true incidence rates for rabies in bat populations are difficult to determine but probably lie somewhere between those obtained from "random" and publicly submitted samples. As the prevalence rate obtained from the IDPH data (6\%) is equaled by the INHS rate for the same period, use of the INHS data for comparisons among species, sex, age and geographic groups appears to be justified.

## Species, sex and age differences

Although opportunities for intraspecific transmission appear to be greater among colonial species (Baer, 1975), the higher prevalences among non-colonial species observed in Illinois (Table l) are consistent with the findings of other studies (Richardson et al., 1966; Birney and Rising, 1967; Baer and Adams, 1970; Whitaker and Miller, 1974; Bigler et al., 1975; Kurta, 1979; Schowalter, 1980; Steece et al., 1982; Pybus, 1986). Three explanations have been suggested as the biological basis for higher rabies prevalences in the non-colonial species. First, some studies have suggested that non-colonial bats with rabies are more prone to attack other bats than are colonial species, which seldom become violent when rabid (Baer, 1975; Bell, 1980; Kaplan, 1985). Although certain normal bat behaviors can be easily misinterpreted as unprovoked attacks, a higher propensity to attack among some species may exist and could allow the disease to spread more readily within their populations. However, Trimarchi (1979) and Schowalter (1980) describe several cases in which rabid colonial bats attacked other animals, including bats and humans. Second, panels of monoclonal antibodies to the nucleocapsid proteins of rabies virus isolates have been used recently to demonstrate the presence of several distinct strains of the virus among bat species in North America (Smith et al., 1986). Thus, the observed interspecific differences in prevalences may be due to variation among strains of the rabies virus itself. Third, the stress of migration may increase the susceptibility of non-colonial species to the disease or stimulate the manifestation of symptoms. Prevalences obtained from non-colonial species in Illinois did increase during migration periods, but colonial species also increase their movements at these times and they exhibited similar prevalence patterns (Table 3).

The relatively high prevalences observed in non-colonial species may also result, at least partially, from sampling bias.

The colonial species generally roost in buildings, but the non-colonial species normally roost in trees and are hard to detect and capture. Non-colonial bats collected by the public, therefore, are more likely to have been predisposed to capture by disease or illness (Baer, 1975; Pybus, 1986).

The significantly higher infection rate observed in female (6\%) than in male (4\%) bats is difficult to interpret because males had higher prevalences than females in three of seven species and the difference was not consistent among the colonial or the non-colonial species groups (Table 1). The higher gregariousness of female bats might provide an explanation. Few other studies have examined differences in prevalences between the sexes, but where such differences have been investigated, no significance was found (Richardson et al., 1966; Bigler et al., 1975; Pybus, 1986).
The only notable result with regard to sexual differences was the large percentage of males ( $63 \%$ ) in the big brown bat sample, whereas females constituted the majority in the samples of all other species (Table 1). For the colonial species, a bias toward females can be explained by the usual female habit of roosting in maternity colonies in buildings where their probability of human contact is greater than for adult males which roost in smaller groups in varied locations. Male big brown bats, however, commonly roost in relatively accessible places around buildings (Barbour and Davis, 1969; Mills et al., 1975) where they are highly susceptible to capture by people concerned about rabies. Such vulnerability to capture also might make publicly submitted samples of male big brown bats less biased toward sick individuals and might explain the unusually low rabies prevalence (3\%) in this group. Kurta and Matson (1980) found a similar majority of males in big brown bats submitted for rabies testing in Michigan but argued for greater longevity in males as the explanation. In the non-colonial species, the consistently strong sampling bias in favor of females suggests behavioral differences,
possibly related to pregnancy and/or maternal care.

Although differences in rabies prevalences between adults and juveniles were mixed, these differences were consistent within the colonial and non-colonial species groups. Although the differences were not significant, juveniles of the two colonial species with adequate sample sizes (little brown and big brown bats) had higher prevalences than adults (Table 1). Conversely, juveniles of the two non-colonial species with adequate samples (hoary and red bats) had significantly lower prevalences than adults. Two types of sampling bias may explain these differences. First, the sample of non-colonial juveniles included a higher proportion of very young bats (collected with their mothers) than the sample of colonial juveniles. Constantine (1986) found that newborn bats may acquire infection at or shortly after from birth from infected mothers but found no reliable evidence that prenatal infection occurs in bats. Thus, a higher proportion of the juveniles in the non-colonial sample may not have had time to contract the disease. Second, because colonial bats generally rear their young in buildings, juveniles of these species that become debilitated with rabies may be more prone to human encounters than are rabid juveniles of non-colonial species that roost in trees.

## Long-term trends

The lack of evidence for long-term trends in rabies prevalences among Illinois bats found in this study supports Baer's (1975) suggestion that the increase in the number of reports of rabid bats in North America reflects greater interest in rabies rather than a true increase. The cyclic nature of rabies in some wildlife species has been widely discussed (e.g., Pool and Hacker, 1982; Bacon, 1985), but most studies of insectivorous bat rabies in North America do not provide data of adequate duration to detect multi-annual cycles. Some studies have failed to detect signif-
icant differences among years (Kurta, 1979; Steece et al., 1982). In contrast, Pybus (1986) found significant differences among years but concluded that rabies is enzootic at relatively constant levels. Although the data from Illinois revealed significant differences among years, the annual variation was relatively small and is consistent with Pybus's (1986) conclusion.

## Seasonal trends

The seasonal variation in the prevalence of bat rabies found in Illinois resembles the pattern of winter lows and summer highs found in several similar studies (Richardson et al., 1966; Constantine, 1967; Whitaker and Milller, 1974; Bigler et al., 1975; Kurta, 1979; Schowalter, 1980; Pool and Hacker, 1982; Steece et al., 1982; Pybus, 1986). The results from Illinois show that not only does the number of reported rabies cases follow an annual cycle but that the rate of reported rabies infection does as well (Fig. 3). Beyond this widely observed trend, these data show a distinct drop in the infection rate during early summer. This decline coincides with the influx of juveniles into the sample and may represent a period during which few young have developed the disease. Additionally, juveniles that are beginning to leave the roost are poor flyers and are more likely to be captured.

## Geographic patterns

The observation that publicly submitted bats in Illinois originated primarily near urban centers is consistent with the findings of other studies (Pool and Hacker, 1982; Pybus, 1986). The absence of specimens from the north-central part of the southern region (Fig. 4) is accounted for by the failure of the laboratory in that region to send specimens to INHS. The high number of non-colonial species obtained from Cook County corresponds with a similar finding in New York City and suggests a greater tendency for these species to take refuge in buildings when they are moving through cities than when they are in rural areas.

Figure 5 shows that bat rabies occurs throughout Illinois but that prevalences in publicly submitted animals have been low in most counties. The only major exception is the three-county area near the southern tip of the state. Closer examination revealed that $59 \%$ ( 22 of 37 ) of the rabid bats from this three-county area were submitted in just two consecutive years (1982 to 1983) during which time the overall prevalence rate for the area was $26 \%$ ( 22 of 84 ) compared with $10 \%$ ( 15 of 133) for the same area in all other years. During the 1982 to 1983 period, big brown bats in the three-county area exhibited a rabies prevalence of $14 \%(n=21)$ versus $7 \%$ ( $n$ $=116$ ) in the remainder of the state; red bats exhibited corresponding prevalences of $36 \%(n=33)$ and $6 \%(n=64)$. The other species had inadequate sample sizes $(<10)$ to make this comparison. Although sampling biases may have occurred and the sample sizes were small, these data were based on bats from several towns in three counties and support the idea that local outbreaks of bat rabies occur (Schowalter, 1980).

In conclusion, rabies prevalences obtained from publicly submitted bats in Illinois indicate that the vast majority of these bats are not rabid and that bat rabies is not increasing. Because a small percentage of bats in this study tested positive for rabies, however, people in Illinois should avoid bat bites and immediately have a rabies test done on any bat that bites a person or pet.

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