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RABIES SURVEILLANCE AMONG BATS IN TENNESSEE, USA, 1996–2010

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ABSTRACT: Rabies virus (RABV) infects multiple bat species in the Americas, and enzootic foci perpetuate in bats principally via intraspecific transmission. In recent years, bats have been implicated in over 90% of human rabies cases in the US. In Tennessee, two human cases of rabies have occurred since 1960: one case in 1994 associated with a tricolored bat (*Perimyotis subflavus*) RABV variant and another in 2002 associated with the tricolored/silver-haired bat (*P. subflavus*/*Lasionycteris noctivagans*) RABV variant. From 1996 to 2010, 2,039 bats were submitted for rabies testing in Tennessee. Among 1,943 bats in satisfactory condition for testing and with a reported diagnostic result, 96% (1,870 of 1,943) were identified to species and 10% (196 of 1,943) were rabid. Big brown (*Eptesicus fuscus*), tricolored, and eastern red (*Lasiurus borealis*) bats comprised 77% of testable bat submissions and 84% of rabid bats. For species with five or more submissions during 1996–2010, the highest proportion of rabid bats occurred in hoary (*Lasiurus cinereus*; 46%), unspecified *Myotis* spp. (22%), and eastern red (17%) bats. The best model to predict rabid bats included month of submission, exposure history of submission, species, and sex of bat.
Key words: Bat, exposure, rabies, surveillance.

INTRODUCTION

Rabies is a fatal zoonosis caused by infection with negative-sense single-stranded RNA viruses of the genus *Lyssavirus*. Among 14 recognized lyssaviruses, only rabies virus (RABV) occurs in the Americas, and the majority of human infections are associated with exposure to bats (Messenger et al. 2002; Schneider et al. 2009). Rabies virus is principally transmitted through bite contact with the saliva of an infected host, and enzootic and epizootic foci occur among bat and carnivore reservoirs. In the US, domestic animal vaccination control programs and public education have dramatically reduced the number of human rabies cases (Smith 1996) and led to the recent elimination of canine RABV transmission (Velasco-Villa et al. 2008). However, an average of two to four cases of indigenously acquired human RABV infections occur annually in the US, and greater than 90% of cases were associated with bat RABV variants (Messenger et al. 2002; Petersen and Rupprecht 2011).

Rabies in North American bats was first detected in a yellow bat (*Lasiurus intermedius*) from Florida in 1953 (Venters et al. 1954). Thereafter, infections have been detected in 33 of the 46 bat species indigenous to the US (Mondul et al. 2003; Constantine 2009). Rabies is enzootic in bat reservoirs and primarily maintained through intraspecific transmission cycles, yet the natural epizootiology and perpetuation of RABV in bat populations remain poorly understood (Hayman et al. 2013). Despite the evolution of species-adapted RABV variants (Smith et al. 1995; Streicker et al. 2012), one study revealed varying levels of asymmetric cross-species

RABV transmission among bats in the US (Streicker et al. 2010). Despite the presence of multiple bat reservoirs of RABV in North America, the majority of human infections in the US are associated with RABV variants of tricolored (*Perimyotis subflavus*), silver-haired (*Lasionycteris noctivagans*), and Brazilian free-tailed (*Tadarida brasiliensis*) bats (Messenger et al. 2002; Petersen and Rupprecht 2011).

In Tennessee there have been two human cases of rabies. The first case, in November 1994, involved a 42-yr-old woman from Cumberland County who did not report any contact with bats (Centers for Disease Control and Prevention [CDC] 1995). Typing of postmortem samples implicated a tricolored bat RABV variant (Messenger et al. 2002). The second case, in August 2002, involved a 13-yr-old male from Franklin County who had contact with a bat found on the ground (CDC 2002). Typing of postmortem samples revealed a tricolored/silver-haired bat RABV variant. In the eastern US, the majority of human RABV infections are associated with the tricolored bat variant (Messenger et al. 2002). Bat RABVs do not appear to be a significant source of domestic animal or wildlife infections in the US (McQuiston et al. 2001; Mayes et al. 2013). However, bat RABVs share a common ancestor with at least three RABV lineages maintained in carnivores (i.e., Mexican skunk, south central skunk, and raccoon variants), and spillover of bat RABV led to independent epizootics in striped skunks (*Mephitis mephitis*) and gray foxes (*Urocyon cinereoargenteus*) in Flagstaff, Arizona (Leslie et al. 2006; Kuzmin et al. 2012).

Bats submitted to public health laboratories for diagnostic testing and recommendations regarding postexposure prophylaxis (PEP) contribute substantially to our understanding of human contact with bats and rabies in the US (Pape et al. 1999). Surveillance of bat rabies across the US has demonstrated consistent seasonal patterns (Constantine 1967; Brass 1994) as well as regional and species level variation in the proportion of rabid bats among submissions (Mondul et al. 2003; Patyk et al. 2012). Some peridomestic bat species are submitted annually in high numbers for passive surveillance yet have low proportions of rabid specimens (e.g., little brown bats, *Myotis lucifugus* and big brown bats, *Eptesicus fuscus*), whereas forest-dwelling bats are submitted in much lower numbers but have markedly higher proportions of rabid specimens (e.g., hoary bats, *Lasiurus cinereus* and silver-haired bats) (Klug et al. 2011). Furthermore, the species composition of bat submissions varies by state and region (Childs et al. 1994; Pape et al. 1999; Parker et al. 1999; Mayes et al. 2013) and may reflect the natural geographic range and abundance of certain bat species across the US, although the criteria for submission of bats for laboratory diagnosis varies among states and could influence apparent geographic trends (Patyk et al. 2012).

Detection of rabid bats through passive surveillance in the US relies on the submission of bats to state public health laboratories, typically following exposure of a pet or human to the bat (CDC 2008). However, exposure data are not frequently included in the regional or national analysis of bat rabies trends. We evaluated geographic, annual, seasonal, gender, age, and species-level trends in bat rabies based on submission of bats to public health laboratories in Tennessee over 15 yr along with associated human or domestic animal exposure history.

MATERIALS AND METHODS

Data collection

The public submitted 2,039 bats for diagnostic testing in Tennessee during 1996–2010. One of four public health laboratories in Knoxville, Nashville, Jackson, or Johnson City tested specimens in satisfactory condition for rabies by the direct fluorescent antibody test on brain tissue impressions. The Johnson City laboratory was closed in 1998 and the testing responsibility for that region was transferred to the Knoxville laboratory. Bats were identified to species using two dichotomous keys

(Schwartz and Schwartz 1981, Menzel et al. 2002) following taxonomy of the third edition of Wilson and Reeder's *Mammal Species of the World* (Simmons 2005). Bats were aged as adult or subadult based on the degree of fusion of the distal epiphysis (Anthony 1988).

We excluded from further analysis 87 specimens unsatisfactory for testing, seven with a missing test result, and two non-native Egyptian fruit bats (*Rousettus aegyptiacus*) from a zoologic collection, yielding 1,943 records. We coded data marked as unknown, such as species of bat, exposure history, and gender or age of bat, as missing data. We classified exposure history responses in four levels: 1) [human, animal, or unspecified] bite, 2) [human, animal, or unspecified] nonbite, 3) [human or animal] unspecified exposure, or 4) no exposure reported. We classified seasons in 3-mo intervals: spring (March–May), summer (June–August), autumn (September–November), and winter (December–February). We compared proportions of rabid bats by species in this study to species-level proportion estimates of rabid bats among submissions from national passive surveillance data during a similar period (Mondul et al. 2003; Patyk et al. 2012).

Statistical analyses

We performed statistical analyses in SAS v9.2 (SAS Institute, Cary, North Carolina, USA). We calculated the proportion of rabid bats among submissions, by species, with exact 95% confidence intervals on proportions. We used a logistic regression model to test for associations between a positive rabies test result and lab of testing, year of submission, month of submission, season of submission, species of bat, sex, age (adult, subadult), and exposure history. We treated unidentified bats and bats identified as *Myotis* spp. as missing data for species. We reassigned 16 records from the Johnson City laboratory to the Knoxville laboratory for analyses. We evaluated combinations of factors in a series of hierarchical models and scored the Akaike information criterion (AIC) for each model (Burnham and Anderson 2002). We considered the (best) minimum adequate model as the model with the lowest AIC value. We used a linear regression analysis to test for correlation between human population size of a county (from census records in 2000; US Census Bureau 2012) and the number of submissions and the number of rabid bats, to investigate whether human or domestic animal contact (i.e., submissions) and number of rabid bats are higher in places of greater human population, at a significance level of $\alpha=0.05$.

RESULTS

A total of 1,870 bats were identified to species, comprising 96% of 1,943 testable bats that were submitted to the Tennessee state health laboratories during 1996–2010 (Table 1). The number of submissions and number of rabid bats were uneven among counties (Fig. 1). Rabies was diagnosed in 10% of the 1,943 testable bats with big brown, tricolored, and eastern red bats (*L. borealis*) accounting for 77% (1,501 of 1,943) of testable submissions and 84% (165 of 196) of rabid bats (Table 1). For species represented by five or more submissions during 1996–2010, highest proportions of rabid bats were observed among hoary, unspecified *Myotis* spp., and eastern red bats, with low proportions of rabid bats among evening (*Nycticeius humeralis*), little brown, silver-haired, and big brown bats (Table 1).

Data for model testing were available for 1,943 submission records. Single factor testing revealed that month was a better predictor than season in terms of capturing seasonal dynamics, and thus subsequent models included month only (Table 2). Predictors of rabid submissions in the best model include: month of submission, bat species, exposure history of submission, and sex of bat (Table 2). Six other models were comparable in AIC score to the best model ($\Delta_i \leq 2$; Table 2). In comparing the candidate models, the sex and age of the bat and lab of testing did not strongly leverage the model score.

An average of 84 (range: 70–102) bats were submitted annually during 1996–2001, with this number increasing to over 200 (range: 206–208) bats during 2002–03 before declining to an average of 146 (range: 112–170) bats during 2004–10. For annual submission data from 1996 to 2010 (Fig. 2), the greatest proportion of rabid bats was observed during 2002 (14%, 29 of 208) and the lowest proportion

TABLE 1. Rabies among bats submitted to the Tennessee Department of Health, 1996–2010. Percent rabid (95% confidence intervals) from this study compared with percent rabid from two national studies.

Species	No. of submissions	No. rabies positive	% Rabid	% Rabid: Mondul et al. 2003 (1993–2000)	% Rabid: Patyk et al. 2012 (2001–09)
Big brown bat (*Eptesicus fuscus*)	692	39	5.6 (4.1–7.6)	5.8	4.7
Brazilian free-tailed bat (*Tadarida brasiliensis*)	2	0	0[a]	31.8	41.5
Eastern red bat (*Lasiurus borealis*)	558	94	16.9 (14.0–20.2)	9.0	14.9
Eastern small-footed bat (*Myotis leibii*)	5	0	0	0	0
Evening bat (*Nycticeius humeralis*)	89	1	1.1 (0.2–6.1)	9.7	3.7
Gray bat (*Myotis grisescens*)	48	0	0	n.d.[b]	0
Hoary bat (*Lasiurus cinereus*)	35	16	45.7 (30.5–61.8)	38.2	35.3
Indiana bat (*Myotis sodalis*)	1	0	0	0	9.1
Little brown bat (*Myotis lucifugus*)	92	2	2.2 (0.6–7.6)	1.7	2.2
Myotis (unspecified) (*Myotis* spp.)	18	4	22.2 (9.0–45.2)	6.1	4.9
Northern long-eared bat (*Myotis septentrionalis*)[c]	34	0	0	n.d.	4.5
Rafinesque's big-eared bat (*Corynorhinus rafinesquii*)	2	0	0	n.d.	0
Silver-haired bat (*Lasionycteris noctivagans*)	60	2	3.3 (1.0–11.4)	12.9	8.3
Southeastern myotis (*Myotis austroriparius*)	1	1	100 (2.5–100)	n.d.	5.3
Tricolored bat (*Perimyotis subflavus*)	251	32	12.8 (9.2–17.4)	17.1	13.7
Unidentified	55	5	9.0 (3.9–19.6)	n.d.	n.d.
Total	1,943	196	10.1 (8.8–11.5)		

[a] The confidence interval was not calculated.

[b] n.d. = not determined.

[c] Reports for *Myotis keenii* were considered *Myotis septentrionalis*.

during 2003 (5%, 10 of 206). The higher proportion of rabid bats during 2002 is reflected in higher proportions of rabid big brown (11% in 2002 vs. 5% across all years), eastern red (23% in 2002 vs. 17% across all years), and silver-haired (13% in 2002 vs. 3% across all years), but not of tricolored bats (10% in 2002 vs. 13% across all years). These four species comprised 85% of submissions and 89% of rabid bats during 2002. When yearly submissions were stratified by exposure history, the peak of submissions during 2002 was driven by greater cases of nonbite exposures or cases with no reported exposure (Fig. 3).

Submissions varied seasonally, with the lowest numbers of bats submitted during winter (mean: 50, range: 42–64), greater numbers during spring (mean: 151, range: 94–191) and autumn (mean: 137, range: 50–230), and highest numbers during summer (mean: 310, range: 278–348). Among monthly bat submissions (Fig. 4), the proportion of rabid bats was highest during September (20%, 45 of 230) and August (18%, 56 of 304) and lowest during February (0%, 0 of 42) and March (1%, 1 of 94). When monthly submissions were stratified by exposure history, nonbite exposures accounted for the majority of submissions in all months, with a peak during July (Fig. 5). Partitioning of the monthly submission data by bat age demonstrated that peaks during June and July were explained by an increase in subadult submissions whereas adults comprised the majority of submissions and rabid bats during autumn (data not shown). Partitioning of the monthly submission data among

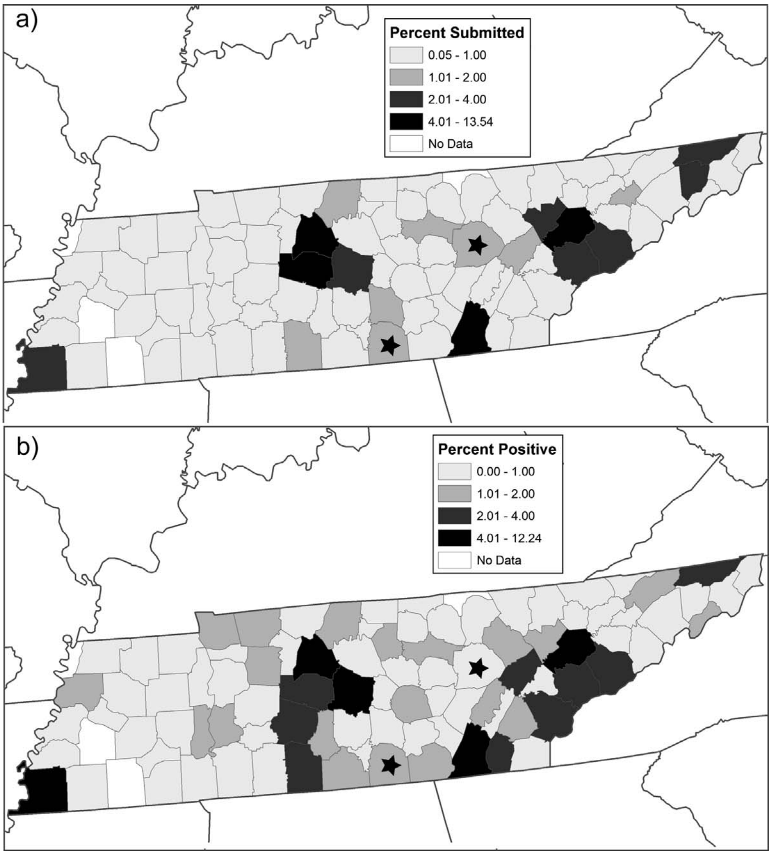

FIGURE 1. Percent contribution for each Tennessee (USA) county toward total (a) submissions and (b) rabid bats, 1996–2010. Two counties where bat-associated human rabies cases have occurred are shown with black stars.

the three main species submitted in Tennessee (*E. fuscus*, *L. borealis*, and *P. subflavus*) revealed that trends in the monthly number of submissions and proportion of rabid bats varied by species (Fig. 6).

For submissions with a reported exposure history (Table 3), there were higher proportions of rabid bats associated with a bite or unspecified exposure, with lower proportions of rabid bats following a non-bite exposure. For cases with a reported exposure, level of risk of encountering a rabid bat varied by species (Table 3).

Human population size (i.e., year 2000) was correlated positively with the number of bat submissions and number of rabid bats reported by county ($P<0.001$). Identical results were obtained using census data from 2005 (data not shown).

DISCUSSION

Species level proportions of rabid bats among submissions in this study were consistent with national estimates (Mondul et al. 2003; Patyk et al. 2012; Table 1). While some areas of the US have dramatically higher submission rates of bats per human population (Patyk et al. 2012), it is unclear whether this reflects a real geographic difference in the incidence of exposure to bats. Regardless, data generated from passive surveillance are highly sensitive to human presence and behavior, as supported by associations between the

TABLE 2. Model fitting and selection for rabies risk among bat submissions (n=1,943) to the Tennessee Department of Health, 1996–2010. The best model is shown in boldface. Additional adequate models (Δ_i<2) are italicized.

Model	K[a]	−2logLik[b]	AIC[c]	Δ_i[d]
Month, species, exposure, sex	32	1,036.838	1,100.838	0
Month, species, exposure, lab, sex	35	1,030.869	1,100.869	0.031
Month, species, exposure, lab	33	1,034.980	1,100.980	0.142
Month, species, exposure	30	1,041.164	1,101.164	0.326
Month, species, exposure, age	32	1,037.240	1,101.240	0.402
Month, species, exposure, lab, age	35	1,031.329	1,101.329	0.491
Month, species, exposure, lab, age, sex	37	1,028.294	1,102.294	1.456
Month, species, age	28	1,048.415	1,104.415	3.577
Month, species	26	1,052.566	1,104.566	3.728
Month, species, lab	29	1,047.084	1,105.084	4.246
Month, species, sex	28	1,049.218	1,105.218	4.380
Month, species, exposure, lab, age, sex, year	51	1,018.231	1,120.231	19.39
Species	15	1,148.241	1,178.241	77.40
Month	12	1,183.106	1,207.106	106.3
Season	4	1,238.406	1,246.406	145.6
Exposure	5	1,256.506	1,266.506	165.7
Lab	4	1,259.625	1,267.625	166.8
Sex	3	1,265.158	1,271.158	170.3
Age	3	1,265.201	1,271.201	170.4
Year	15	1,253.375	1,283.375	182.5

[a] Number of estimated parameters.

[b] Negative two times the log-likelihood.

[c] AIC = Akaike information criterion score.

[d] Difference in AIC score from best model.

population size of a county and the number of submissions and rabid bats detected in this study and by results from a Texas study reporting higher submissions and numbers of rabid bats from urban compared with rural localities (Mayes et al. 2013). Despite this observation, the two bat-associated human rabies cases in Tennessee did not occur in counties with the highest number of submissions or rabid bats (Fig. 1).

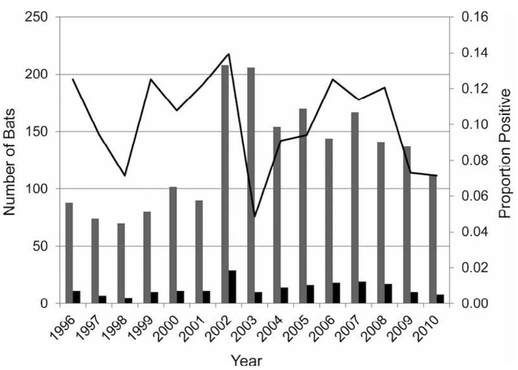

FIGURE 2. Annual number of bat submissions (gray bars) to the Tennessee Department of Health, number of rabid bats (black bars), and proportion of bats found rabid (solid line),1996–2010.

The 2002 human rabies case in Tennessee likely prompted higher numbers of bat submissions during 2002–03, and the spike in submissions that followed this case reflected an increase in nonbite exposure cases (Fig. 3). Similar spikes in bat submissions followed a human case in Texas during 2006, further supporting the impact of increased media attention and educational awareness on public submissions of bats (Mayes et al. 2013). The greatest proportion of rabid bats was detected during 2002, although it is unclear whether this trend has any relationship to the occurrence of the human case that same year. At the national level, 2002 was not an exceptional year for rabies submissions or proportional detection of rabid bats (Patyk et al. 2012). The

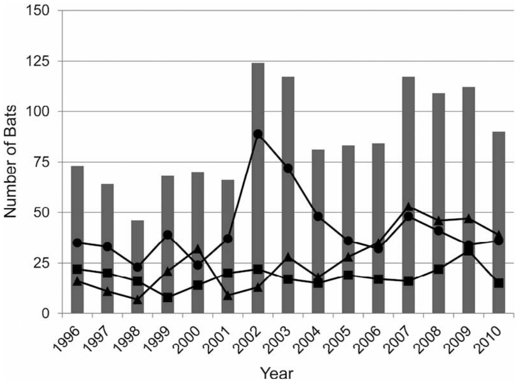

FIGURE 3. Annual number of bat submissions (gray bars) to the Tennessee Department of Health, stratified by reported exposure history including bite (squares), nonbite (circles), and unspecified (triangles) human or pet exposures, 1996–2010.

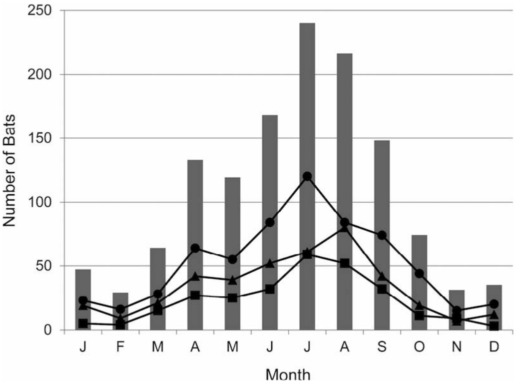

FIGURE 5. Monthly number of bat submissions (gray bars) to the Tennessee Department of Health, stratified by reported exposure history including bite (squares), nonbite (circles), and unspecified (triangles) human or pet exposures, 1996–2010.

estimated proportion of rabid bats among submissions was lowest in 2003 and may be due to a dilution effect resulting from greater public awareness and submission of bats following the 2002 human rabies case, as submissions stabilized to lower levels during 2004 and subsequent years.

As demonstrated in various studies (Constantine 1967; Brass 1994; Mondul et al. 2003), the submission of bats and proportion of rabid bats among submissions is highly seasonal, and month of submission was a key predictor of rabid bats. The high number of submissions during summer reflected a proportionally higher number of nonbite exposures and an increase in subadult submissions. Overall submissions of bats and the proportion that were rabid tend to be highest during August and September, though trends varied among commonly submitted species (Fig. 6). Big brown bats have several peaks in the proportion of rabid bats among submissions throughout the year in Tennessee, notably during April (12%, 5 of 41), July (9%, 11 of 120), and August (9%, 11 of 129). Big brown bats exhibit synchronized parturition during early June each year, with females giving birth to one or two young (Kurta and Baker 1990). The nursing period generally lasts from early June until the end of July, when young become weaned and volant. During autumn, swarms gather for mating and short-distance migration between summer maternity colonies and winter hibernacula (Kurta and Baker 1990; Neubaum et al. 2006). Big brown bats typically hibernate during the winter months in caves or buildings, and the peak in the proportion of rabid bats observed during April may relate to infections that have overwintered in the bats and are reactivating following arousal from hibernation and increased activity during March–April (Sulkin and

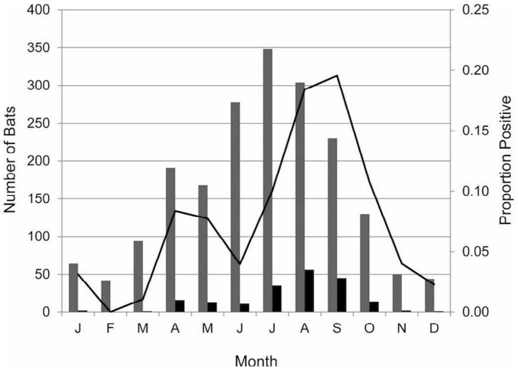

FIGURE 4. Monthly number of bat submissions (gray bars) to the Tennessee Department of Health, number of rabid bats (black bars), and proportion of bats found rabid (solid line), 1996–2010.

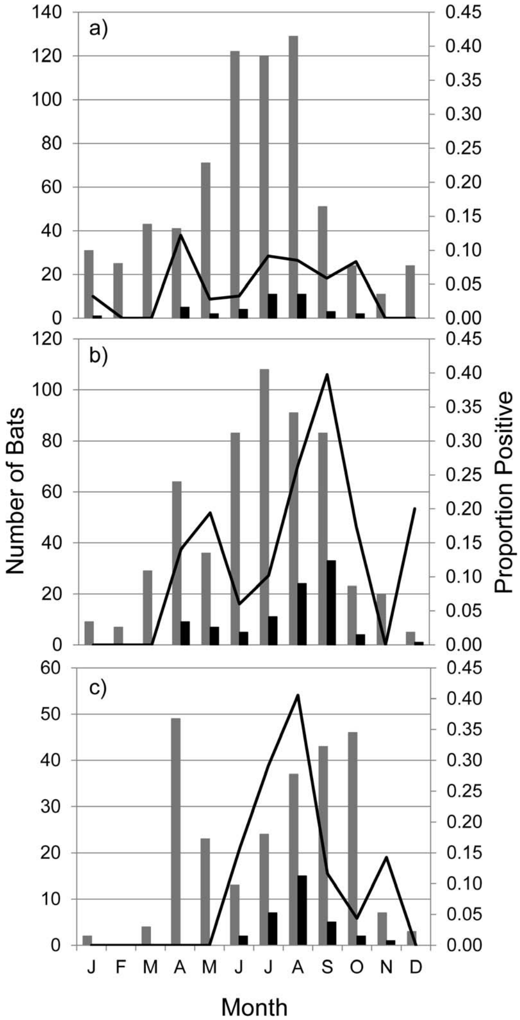

FIGURE 6. Monthly number of submissions (gray bars) to the Tennessee Department of Health, number of rabid bats (black bars), and proportion of bats rabid (solid line) during 1996–2010 among (a) big brown bats, (b) red bats, and (c) tricolored bats.

Allen 1974; George et al. 2011). Thus, peak proportions of rabid big brown bats are, with incubation period time lags taken into consideration, consistent with critical life history transitions in this species.

Among eastern red bats, peaks in the proportion of rabid bats were observed during August (26%, 24 of 91) and September (40%, 33 of 83) with a smaller peak during early spring. Eastern red bats are tree-roosting, solitary bats but also give birth in mid-June to litters of one to five pups, with young weaned and volant by 6 wk following parturition (Shump and Shump 1982). Breeding and migration also occur during August and September, although eastern red bats migrate much longer distances compared with big brown or tricolored bats, and eastern red bats utilize trees or leaf litter for winter hibernation. Peak proportions of rabid eastern red bats appear most consistent with spring arousal and seasonal birth pulses.

Tricolored bats also had peaks in the proportion of rabid bats occurring during July (29%, 7 of 24) and August (41%, 15 of 37). Timing of parturition appears to vary considerably by latitude in tricolored bats and is suggested to occur later and be more synchronized in northern populations (Fujita and Kunz 1984). In the southeastern US, parturition may occur during mid to late June, with females giving birth to twins, although postnatal growth may be more rapid in this species compared with eastern red and big brown bats (Fujita and Kunz 1984). However, tricolored bats also gather for mating during autumn and migrate to winter hibernacula, typically caves (Fujita and Kunz 1984). Peak proportions of rabid tricolored bats appear most consistent with the seasonal birth pulse but do not show signatures of infections resulting from springtime arousal following hibernation in this study.

Physiologic and behavioral drivers of the seasonal epizootiology of RABV in bats in the US undoubtedly include arousal following hibernation (George et al. 2011) and synchronized parturition in colonial species (Turmelle et al. 2010), as well as the short- and long-distance migration during autumn that is characteristic of most temperate bat species (Fleming and Eby 2003; Dimitrov and Hallam 2009). Longitudinal and comparative studies are needed to elucidate factors influencing the seasonal force of RABV infection in ecologically diverse bat communities (Hayman et al. 2013).

TABLE 3. The exposure route (i.e., bite, nonbite, unspecified) among bat species represented by >5 submissions to the Tennessee Department of Health, 1996–2010, with a reported exposure to a human or pet. Proportional frequency of a given exposure route, among total known exposure cases for a species, is shown in parentheses.

Species	Bite exposure cases	Proportion rabid – bite exposures	Nonbite exposure cases	Proportion rabid – nonbite exposures	Unspecified exposure cases	Proportion rabid – unspecified exposures	Total cases with known exposure
Big brown bat (*Eptesicus fuscus*)	99 (0.21)	0.04	211 (0.45)	0.06	157 (0.34)	0.06	467
Eastern red bat (*Lasiurus borealis*)	94 (0.23)	0.20	187 (0.47)	0.12	119 (0.30)	0.24	400
Evening bat (*Nycticeius humeralis*)	12 (0.19)	0	33 (0.52)	0.03	18 (0.29)	0	63
Gray bat (*Myotis grisescens*)	5 (0.21)	0	6 (0.25)	0	13 (0.54)	0	24
Hoary bat (*Lasiurus cinereus*)	6 (0.22)	0.67	13 (0.48)	0.31	8 (0.30)	0.63	27
Little brown bat (*Myotis lucifugus*)	7 (0.11)	0	38 (0.62)	0.03	16 (0.26)	0	61
Northern long-eared bat (*Myotis septentrionalis*)	7 (0.29)	0	14 (0.58)	0	3 (0.13)	0	24
Silver-haired bat (*Lasionycteris noctivagans*)	9 (0.20)	0.11	25 (0.54)	0	12 (0.26)	0	46
Tricolored bat (*Perimyotis subflavus*)	19 (0.14)	0.37	78 (0.56)	0.15	41 (0.30)	0.15	138
Total	258 (0.21)	0.14	605 (0.48)	0.09	387 (0.31)	0.13	1,250

Species composition of submissions in Tennessee was similar to that reported for other states in the southeastern US, where submissions were predominantly big brown and eastern red bats. However, tricolored bats were more frequently submitted in Tennessee compared with neighbor states Alabama and South Carolina (Parker et al. 1999; Hester et al. 2007). Bat species was a key predictor of rabid bats and the highest proportion was observed among lasiurine bats. These results likely reflect differences in bat roosting ecology (Klug et al. 2011). Bats that come into contact with the public may be more likely to be sick and behaving unnaturally, particularly among inconspicuous species. Among the three most frequently encountered bats (i.e., species with highest submission rates), contact with eastern red and tricolored bats may carry greater risk, as the proportion of rabid bats is greater among submissions of these two species (17% and 13%, respectively) when compared with big brown bats (5%).

Submissions varied in the types of exposures reported across bat species, and exposure history was a key variable predicting rabid bats. Nonbite exposures accounted for the majority (48%) of submissions, with unspecified exposures and bite exposures accounting for fewer submissions (31% and 21%, respectively). Nonbite exposures were also responsible for the majority of submissions annually and by month, similar to studies of bat rabies in Colorado and Texas (Pape et al. 1999; Mayes et al. 2013). The risk of contact with rabid bats was highest for bite exposures and is similar to results obtained from a Colorado study (Pape et al. 1999), yet the risk of contact with rabid bats was also high in this study among cases where exposure was reported but unspecified (Table 3). Exposure to rabid bats following bite contact was higher than average when the exposure involved eastern red, hoary, and tricolored bats, and lower than average when contact involved big brown and silver-haired bats. Current recommendations suggest that any exposure to a bat be thoroughly assessed in regard to the need for PEP (CDC 2008). Persons are advised to seek medical attention following a bite exposure or uncontrolled contact with a bat unless the animal was submitted for diagnostic testing and confirmed to be negative. The apparent variation in risk between exposures to tricolored and silver-haired bats in this study may be explained by geography, with a greater risk of infection with tricolored bat RABV variant in the eastern US and the silver-haired bat RABV variant in the western US (Messenger et al. 2002). The substantial proportion of rabid bats with unspecified exposure history in this study highlights the importance of carefully evaluating possible human and domestic animal exposures. Additionally, it is important to advise the public not to touch or handle bats. However, in circumstances where a person is trying to safely remove a bat from a dwelling or capture it for testing, it is highly recommended to use or wear some form of barrier protection (shoe box, leather gloves, etc.). Although domestic animals are at a greater risk of acquiring RABV infection from mesocarnivores, based upon surveillance data and viral characterization, rabies in bats is more geographically widespread across the US and can be transmitted by a variety of species, thus highlighting that all pets should be current on rabies vaccination to avoid scenarios requiring animal euthanasia for diagnostic testing and to minimize the risk of humans acquiring this highly fatal disease.

This study is an important baseline metric due to the recent incursion of White Nose Syndrome (WNS) into bat populations of the southeastern US. A recent article reported detection of *Pseudogymnoascus destructans*, the causative agent of WNS, on bats in Tennessee during 2012–14 (Bernard et al. 2015), although detections first appeared in Tennessee during the winter of 2009–10 (US Fish and Wildlife Service 2015). While the geographic scope of this study is limited, the study area includes Great Smoky Mountains National Park, which has the highest number of visitors of any national park in the US. Furthermore, also near the study area is Mammoth Cave National Park (MCNP), where there are regular tours of caves inhabited by bats. The National Park Service published a podcast on 26 March 2015 warning of an increased number of bats being found in conspicuous areas of MCNP. The effects of WNS on bat populations may lead to greater numbers of human and domestic animal encounters with bats on the landscape in this region, especially at caves, and to greater numbers of cases requiring evaluation by public health officials.

Monoclonal antibody or genetic typing was not routinely performed on the rabid bats in this study, which limits our understanding of the impact of spillover RABV infections in Tennessee bat populations. However, 12% (24 of 196) of rabid bats in this study were included in a bat RABV cross-species transmission study by Streicker et al. (2010). A single spillover infection was detected among 24 Tennessee bats collected during 2004–05, where an eastern red bat RABV lineage was documented in a little brown bat. Streicker et al. (2010) found that eastern red and other lasiurine bats were frequently donors of RABV infections to other bat species. Given the high numbers of submissions and rabid eastern red bats in this study, cross-species transmission undoubtedly impacts RABV circulation among bat populations in Tennessee, although the frequency was 4% (1 of 24) in a subset of Tennessee bats (Streicker et al. 2010). A Texas study reported spillover infections in just 2% of 1,922 typed bat rabies cases (Mayes et al. 2013). Whenever possible, routine typing of rabid bats and mesocarnivores can yield additional insight into RABV transmission dynamics in these important wildlife reservoirs.

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