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Apparent annual survival of female eastern small-footed bats (*Myotis leibii*) roosting in Arkansas bridges

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The Eastern Small-footed Bat (*Myotis leibii*) inhabits mountainous areas of the eastern United States and generally roosts in cliff faces and talus slopes. However, the difficulty of accessing these sites has limited research on this species. We studied survival rates of eastern small-footed bats by capturing bats roosting in crevices between sections of concrete guardrails on bridges in the Ozark mountains of northern Arkansas from 2014 to 2021. We accumulated 1,413 bat captures (1,050F; 363M) of 283 individual females and 198 individual males sampled over 8 years and determined apparent annual survival of female bats using Cormack–Jolly–Seber survival models. Only 1 of 30 bats tested positive for the presence of *Pseduogymnoascus destructans*, a fungus causing white-nose syndrome (WNS) which is responsible for significant declines in populations of some North American bat species, when all maternity colonies were sampled in the spring of 2019. Overall apparent annual survival of all females was 0.643, with first-year juvenile survival of 0.472 and adult (ages 1–6) survival of 0.744, approximately 58% greater than first-year survival. Apparent annual survival did not differ greatly among the sites or among years. We found no significant decline or increase in overall number of bats among all sites during the 8 years of study. Stability in both the number of bats encountered and their survival rates suggests that the impact of WNS on these colonies has been marginal.

Key words: Arkansas, banding, bridges, demography, *Myotis leibii*, Ozark, survival

The Eastern Small-footed Bat (*Myotis leibii*) is found in mountainous areas of eastern North American from Ontario southward through the Appalachians and westward to Oklahoma (Best and Jennings 1997). During the summer months, it usually roosts in cliff faces, steep talus slopes, and underneath flat rocks (Johnson and Gates 2008; Whitby et al. 2013; Kearny et al. 2022), although roosting in buildings and bridges has been observed (MacGregor and Kiser 1998; O'Keefe and LaVoie 2011; Sasse et al. 2013). During the winter it hibernates in caves and abandoned mines, often in narrow crevices or sometimes under rocks on the cave floor (Best and Jennings 1997).

Estimates of demographic parameters for bats are relatively rare, yet they are vitally important for understanding population health for these animals that have low reproductive rates and are often threatened or endangered. An important demographic parameter is annual survival rate, especially since the appearance of white-nose syndrome (WNS) in North American bat populations. WNS is a novel disease associated with the fungus *Pseudogymnoascus destructans* (*Pd*), which has caused multiple species of bats to suffer precipitous population declines since its discovery in the United States. Larger bats may survive WNS better than smaller bats (Haase et al. 2020) and two other small bats previously common in this region have experienced serious population declines due to WNS—Northern Long-eared Bat (*M. septentrionalis*) populations dropped by 98% and the Tricolored Bat (*Pipistrellus subflavus*) by 77% (Cheng et al. 2021; Perry and Jordan 2022). The impact of WNS has primarily been assessed based on trends in population estimates derived from surveys conducted in caves during winter hibernation (e.g., Cheng et al. 2021) or from capture rates in mist nets during the summer months (e.g., Johnson et al. 2021). However, in Arkansas the Eastern Small-footed Bat has been observed in only a few caves, usually in small numbers, and is rarely observed in other surveys such as mist netting (Sasse et al. 2013) and the impact of WNS on this species in this state is unknown.

Survival rates of *Myotis* spp. bats in the eastern United States have rarely been examined, with most species being the subject of only one or two studies. Survival rates of adult *Myotis* spp. bats have been found to range from 0.17 to 0.91 (Humphrey and Cope 1977; Keen and Hitchcock 1980; Elder and Gunier 1981; Stevenson and Tuttle 1981; Boyles et al. 2007; Frick et al. 2009). Hitchcock et al. (1984) determined survival rates for eastern small-footed bats based on bats banded inside hibernacula; however, this type of activity can greatly disturb bats and may lead to population declines (Tuttle 1979; Thomas 1995). Studying the population ecology of eastern small-footed bats during the active season is complicated by their use of difficult to access natural roost sites such as cliff faces (Johnson and Gates 2008; Johnson et al. 2011) and small group size (O'Keefe and LaVoie 2011). While they can readily be captured in mist nets near natural roost sites (e.g., Johnson et al. 2011; Huth et al. 2015), in general they are rarely caught during summer mist net surveys (e.g., LaVal and LaVal 1980; Rojas et al. 2017; Reynolds et al. 2021).

Thomson (2013) demonstrated that eastern small-footed bats can be found and easily captured in concrete guardrails on the sides of bridges. Such sites can quickly be surveyed by a single individual without the logistical difficulties and safety issues involved in accessing maternity colonies in cliffs or steep talus slopes, while at the same time eliminating the harm that can occur when capturing bats during hibernation. Our goal was to examine annual survival rates of eastern small-footed bats derived from 8 years of bat banding at summer maternity colonies found in bridges in the Ozark Highlands of Arkansas. We used Cormack–Jolly–Seber (CJS) models (Lebreton et al. 1992) to estimate apparent survival (e.g., Perry and Jordan 2020) of adult and juvenile (first-year) female bats from 2014 to 2021. This project is the first to examine annual survival rates of female eastern small-footed bats derived from sampling of summer maternity roosts and the first to examine survival of eastern small-footed bats roosting in bridges.

Materials and Methods

This study took place in the Ozark mountains of northwest and northcentral Arkansas. Bridges occupied by eastern small-footed bats fell primarily within the Boston Mountain subdivision. This region ranges in elevation from 152 to 823 m and is underlain by Pennsylvanian shales and sandstones characterized by many steep ravines and gorges (Pell 1983; USDA Forest Service 1999). The area is 78% forested, consisting of a mixture of hardwood and mixed pine-hardwood forests (USDA Forest Service 1999).

In the summers of 2013 and 2014, we used a flashlight to survey for bats in the crevices between concrete guardrail segments on the sides of the road deck of 164 bridges. The undersides and other portions of bridges were not surveyed. We identified maternity colonies ($n = 7$) of eastern small-footed bats using 21 bridges in Carroll, Franklin, Johnson, Madison, Newton, Pope, Stone, and Washington counties. We defined a maternity colony as a bridge at which nonvolant juveniles were observed and any bridge subsequently used by bats from this bridge. Therefore, maternity colonies often consisted of multiple bridges that bats moved among during the summer and among years. We surveyed bridges associated with maternity colonies multiple times during the active period (April–October) from 2014 to 2021 and attempts were made to capture all bats during each survey except when nonvolant pups were present, generally in June. Observed bats were captured by hand using a thin metal yardstick to coax them from the crevice. Species, sex, mass (gm), left forearm length (mm), and age class (juvenile or adult) were recorded for all captured individuals. We determined age class based on epiphyseal–diaphyseal fusion (Anthony 1988); however, by August it was generally not possible to discriminate this characteristic and bats initially captured during this period were considered unknown age class. Bats were banded using uniquely numbered 2.4-mm-lipped metal bat bands (Porzana Ltd, East Sussex, United Kingdom). We avoided handling bats during spring of 2020, due to potential human–bat transmission of the SARS-CoV-2 virus but resumed work that summer with the use of facemasks. Records associated with 17 bat captures were excluded from analysis due to probable misreading of bands at the time of capture and one bat was excluded because it died during handling.

We examined number of female bats (adult and juveniles combined) over the 8 years of study to determine if number of bats among all sites declined or remained stable using linear regression analysis (SAS Institute Inc. 2011). To detect the presence of *Pd*, we wiped sterile swabs on the nose and wings of 30 bats (26 females; 4 males) from all maternity colonies during 10–22 April 2019 and submitted these samples to the National Wildlife Health Center (Madison, Wisconsin) to test for the presence of *Pd*. All captures of live bats followed guidelines for the use of mammals in research (Sikes et al. 2016).

We used open-population, CJS models (Lebreton et al. 1992) in program MARK (Cooch and White 2019) to determine apparent survival (ϕ) of female bats and probability of reencountering an individual (p; recapture probability). CJS models estimate "apparent survival" because they cannot distinguish mortality from emigration. We included only female bats in our analyses because juvenile males recruited into the population during the summer maternity season typically do not return to maternity roosts in subsequent years. We combined records from multiple surveys in a year to determine presence/absence of individual bats each year for survival analysis; therefore, survival was calculated as annual apparent survival.

To determine if survival differed among bats in different age classes, we conducted an analysis on a subset of the data that included only bats that were initially banded as juveniles (n = 130 individuals) so that only known-aged bats were included in the analysis; we combined data from all sites. We used this data set to determine survival of juveniles during their first year and survival of adults (ages 2–6) because lower survival in first-year juveniles is common in bats and survival is often age-specific (Davis 1966; O'Shea et al. 2010). We developed and compared eight a priori age and cohort CJS models (Cooch and White 2019) that varied survival and recapture probabilities. For apparent survival (ϕ), we included models where ϕ differed for two age classes (*a*; either adult [age > 1 year old] or juvenile [age < 1 year old]) or all age classes ("age class"; ages 1–6). We also included models where both juvenile and adult ϕ differed over the eight sampling periods (*t*; time) or juvenile ϕ differed over time and adult ϕ was not affected by time. We included detection probability of individuals in our models, which varied by age (*a*; juvenile or adult) or remained constant (.).

We conducted a second modeling effort to examine differences in survival and probability of detection among the different maternity sites (site analysis) using the full data set that contained all females (regardless of age when initially banded; *n* = 254 individuals). We did not include the Stone County or Pope County records in the site analysis because of small sample sizes. For site analysis, we compared nine competing a priori models where apparent survival (ϕ) and recapture probability (*p*) were: (1) held constant over time (.); (2) varied among sample years (*t*); or (3) varied based on maternity site (*s*). We included effects of time (*t*) to determine if survival may have changed over the 8 years of sampling. We did not include interactions (e.g., *t* * *s*) in our model comparisons because initial model sets resulted in confounded models with implausible *SE*s (Cooch and White 2019).

We compared competing models in the two model sets using Akaike's Information Criterion for small samples (AICc; Burnham and Anderson 2002). We then estimated model fit using the variance inflation factor ($\hat{c}$) and estimated the median $\hat{c}$ values; we corrected model AICc values for overdispersal using QAICc (Cooch and White 2019). We considered models within 2 QAICc units of the best model to be in the plausible model set (Burnham and Anderson 2002). If more than one model was in the best model set, we averaged the model parameters to determine ϕ and *p* and we calculated unconditional *SE*s for ϕ and *p* from the best model sets (Burnham and Anderson 2002).

Results

We had 1,413 captures of bats (1,050F; 363M) from 2014 to 2021, comprising 283 individual females and 198 individual males. Maternity colonies comprised of adult females and juveniles (male and female) ranged in size from 1 to 38 bats (Table 1). We found no significant decline or increase in overall number of bats among all sites during the 8 years of study ($F_{1,54}$ = 1.06, *p* = 0.308, r^2 = 0.019). Over the 8 years, the percentage of females captured more than once was 63% and mean number of times an individual female was encountered was 3.71 ± 0.26 (*SE*) (range 1–24). The percentage of female bats captured in more than 1 year was 48.41%. One female captured in spring of 2013 was recaptured every subsequent year of the study and was ≥9 years old, and one male captured in September 2013 was ≥8 years old when recaptured in 2021. Most (66%) males were captured only once and mean number of times a male was encountered was 1.83 ± 0.16 (range 1–18). We conducted 332 survey events where we attempted to capture bats and the mean percentage of bats observed that were captured was 95.52% ± 0.01%, with all observed bats being captured in 82% of surveys. Of the 30 bats we swabbed in spring 2019 to determine the presence of *Pd*, one bat from Stone County was positive for the presence of *Pd*, whereas one bat each from Pope, Washington, and Madison counties tested inconclusive; all other bats tested negative.

Table 1.—Total number of individual adult female and known juvenile (both sexes) eastern small-footed bats encountered in colonies roosting during summer in bridges of northern Arkansas, 2014–2021.

Site	2014	2015	2016	2017	2018	2019	2020	2021
Carroll-Newton County	10	18	15	17	10	9	9	10
Franklin County	8	14	9	17	20	25	13	13
Madison County	30	28	27	38	31	38	30	33
Pope County	0	2	5	23	8	6	7	7
Stone County	6	10	0	1	0	1	0	0
Washington County 1	15	12	10	13	10	6	7	10
Washington County 2	30	29	16	10	8	9	3	5
All sites	99	113	82	119	87	94	69	78

Our models that distinguished bats by age using only known-aged bats that with all sites combined resulted in two models within two units of QAICc (Table 2). These models differentiated apparent survival of adults from first-year juveniles. Models that determined survival by age class (age 1–6) and models that included the effects of time (sample year) on apparent survival (either adult or juvenile) were not in the best model set. Our averaged model from the best model set indicated that both apparent annual survival and probability of detection differed between female adults and female first-year juveniles. Apparent annual survival of first-year juveniles was 0.472 ± 0.089 (unconditional *SE*), whereas apparent annual survival of adults (ages 2–6) was 0.744 ± 0.084, approximately 58% greater than first-year survival. Probability of detection also differed between first-year juveniles and adults, with detection probability being slightly less (0.829 ± 0.089) for juveniles than adults (0.850 ± 0.080).

Our model set that differentiated apparent annual survival and probability of detection of bats among different maternity sites using the full model set (known- and unknown-aged bats) included two models in the best model set (Table 3). No models that included the effects of sample year (*t*) were included in the best model set and both models in the best model set indicated that detection probability (*p*) did not differ among sites or over time. The model that distinguished survival among sites was equally plausible to the model that combined all sites. Therefore, we averaged survival and probability of detection from these two models. Model-averaged parameter estimates indicated that apparent annual survival differed slightly among the sites, ranging from 0.596 at the Washington County 2 site to 0.681 at the Madison County site (14% greater; Table 4). Probability of detection was similar among all sites (0.805 ± 0.031). Based on our model of all sites combined (ϕ[.] p[.]) that was equally plausible, apparent annual survival for all females regardless of site or age was 0.643 (±0.024) and

Table 2.—Comparison of models for annual apparent survival (ϕ) and encounter probability (*p*) for known-age female eastern small-footed bats ($n = 130$ individuals) roosting during summer in bridges of northern Arkansas, 2014–2021, based on differences among time periods (year of sampling; *t*), age (*a*; first-year juveniles [Juv] or Adult), age class (ages 1–6), or no effect of time or age (.). Model comparisons include difference between each model and the model with lowest QAICc (ΔQAICc), model weights (ω_i), model likelihood, number of parameters included, and *Q* deviance for each model.

Model	QAICc	ΔQAICc	Weight (*ωi*)	Model likelihood	No. param.	*Q* deviance
ϕ(*a*) *p*(.)	115.96	0	0.624	1	3	23.405
ϕ(*a*) *p*(*a*)	117.80	1.84	0.249	0.399	4	23.162
ϕ(age class) *p*(.)	119.84	3.88	0.090	0.144	6	20.978
ϕ(age class) *p*(*a*)	121.74	5.78	0.034	0.056	7	20.729
ϕ(Juv[*t*] Adult[.]) *p*(.)	127.21	11.25	0.002	0.004	9	21.838
ϕ(Juv[*t*] Adult[.]) *p*(*a*)	129.02	13.06	0.001	0.002	10	21.438
ϕ(Juv[*t*] Adult[*t*]) *p*(.)	137.37	21.41	0.001	0	14	20.693
ϕ(Juv[*t*] Adult[*t*]) *p*(*a*)	139.23	23.27	0.001	0	15	20.217

overall probability of reencountering a bat was 0.785 (±0.032). Probability of detection in this model set was lower than the models using only bats of known age because bats of unknown age were often detected only once late in the active season and not detected again.

Table 3.—Comparison of models for apparent annual survival (ϕ) and encounter probability (*p*) for female eastern small-footed bats (regardless of age when banded, $n = 254$ individuals) roosting during summer in bridges of northern Arkansas, 2014–2021, based on differences in time periods (year of sampling; *t*), site (*s*; five bridge sites), or no effect in time or site (.). Model comparisons include difference between each model and the model with lowest QAICc (ΔQAICc), model weights (ω_i), model likelihood, number of parameters included, and *Q* deviance for each model.

Model	QAICc	ΔQAICc	Weight (*ωi*)	Model likelihood	No. param.	*Q* deviance
ϕ(*s*) *p*(.)	745.90	0	0.432	1	6	277.657
ϕ(.) *p*(.)	745.99	0.10	0.412	0.953	2	285.904
ϕ(.) *p*(*t*)	750.89	4.99	0.036	0.082	8	278.525
ϕ(*s*) *p*(*s*)	750.89	4.99	0.036	0.082	10	274.365
ϕ(.) *p*(*s*)	751.14	5.24	0.031	0.073	6	282.901
ϕ(*s*) *p*(*t*)	751.46	5.56	0.027	0.062	12	270.738
ϕ(*t*) *p*(.)	751.61	5.72	0.025	0.057	8	279.250
ϕ(*t*) *p*(*t*)	757.88	11.98	0.001	0.003	13	275.042
ϕ(*t*) *p*(*s*)	758.05	12.15	0.001	0.002	12	277.326

Discussion

Our study methods were effective in locating and banding large numbers of bats and providing robust survival estimates for the difficult-to-capture Eastern Small-footed Bat. Our estimate of adult female survival (0.744) was on the high end in comparison to pre-WNS survival rates in other *Myotis* spp. bats, such as Little Brown Bat (*M. lucifugus*; 0.63–90; Frick et al. 2009) and Indiana Bat (0.627; Boyles et al. 2007) but similar to average adult female survival (0.774) derived from multiple species (Lentini et al. 2015). Studies of insectivorous bats typically find survival of juveniles during their first year lower than adult survival (Frick et al. 2009; O'Shea et al. 2010; Lentini et al. 2015; Davy et al. 2022), similar to the results of this study. Our survival rate of juvenile females (0.472) was generally greater than those reported for other *Myotis* spp. bats, such as the Little Brown Bat (0.23–0.46; Frick et al. 2009). Although our modeling of apparent survival could not discern survival from emigration, it is possible that some juvenile females that were not recaptured in later years may have emigrated, which would have lowered our estimates of apparent survival. The failure of most juvenile males to return to their natal colony suggests male-biased dispersal in eastern small-footed bats (Moussy et al. 2013).

We found higher female survival rates than the only previous study of apparent survival in eastern small-footed bats (Hitchcock et al. 1984). Hitchcock et al. (1984) captured bats during hibernation in Ontario and observed annual survival rates of unknown-age females of only 0.421, whereas our annual survival rate for all female bats (regardless of age) was 0.643 (53% greater). Our sample size of female bats (283) was larger than the sample size (120 bats) of Hitchcock et al. (1984) and we used advanced modeling techniques that included controls for detectability, which was likely more accurate than their study. However, differences in populations, location (including surrounding habitats and the more northern latitude of their study), natural versus manmade roosts, and winter disturbance may have affected survival between the two study populations. Among the reasons that Hitchcock et al. (1984) suggested for the low female survival that they observed was the impact of parasites and associated diseases. Although research on the parasites of this species is sparse, previous work conducted on this population indicates that ectoparasites were rare and the endoparasites encountered are not known to be linked with negative effects (Sasse et al. 2016; McAllister et al. 2017).

WNS is known to infect eastern small-footed bats although the impact varies across its range. Early studies on the impact of WNS on this species from summer captures indicated significant declines following the arrival of the disease in New Hampshire and West Virginia (Francl et al. 2012; Moosman

Table 4.—Apparent annual survival (ϕ), probability of detection (p), and unconditional SE_S for both parameters averaged from the best model set for all female eastern small-footed bats roosting during summer at five maternity colonies in bridges (Sites) in northern Arkansas, 2014–2021. All females, regardless of age when banded, were included and probability of detection was similar among sites; effects of sample year were not included in the best models set.

Site	ϕ	*SE*	*p*	*SE*
Carroll-Newton County	0.620	0.053	0.805	0.031
Franklin County	0.661	0.044	0.805	0.031
Madison County	0.681	0.048	0.805	0.031
Washington County 1	0.615	0.059	0.805	0.031
Washington County 2	0.596	0.064	0.805	0.031

et al. 2013). However, analyses over longer periods indicated either little change or slight increases in Eastern Small-footed Bat populations (O'Keefe et al. 2019; Johnson et al. 2021; Reynolds et al. 2021). Their potential resistance to WNS may result from their use of smaller hibernacula sites that limit the number of individuals exposed to WNS. Shorter torpor bouts and regular winter activity (including foraging for food) suggest WNS may not cause additional winter arousals and loss of fat beyond their normal winter behavior (Bernard et al. 2017, 2021; Reynolds et al. 2017; Jackson et al. 2022). This species has also been found roosting near the front of caves and in crevices of rock ledges and other sites exposed to temperatures as low as −9°C during winter where they were more directly exposed to colder winter weather that could inhibit growth of *Pd* (Webb et al. 1996; Johnson et al. 2016; Moosman et al. 2017).

It is not clear what impact WNS may have had on small-footed bat populations in this study. The limited sampling done in the spring of 2019 confirmed *Pd* in only one colony, although three other colonies had bats with inconclusive results for presence of *Pd*. Monitoring of winter hibernacula utilized by other species found *Pd* or WNS present in various bat species in Franklin, Madison, Newton, Stone, and Washington counties of Arkansas from 2013 to 2015. WNS or *Pd* was not detected in Pope, Johnson, and Carroll counties during the study (White-Nose Syndrome Response Team 2022) with the exception of an inconclusive *Pd* sample we collected in Pope County in 2019. Although WNS was widespread in the mountainous regions of Arkansas and has caused significant declines in some species such as the Northern Long-eared Bat (Edmonds 2020; Perry and Jordan 2022), our results suggest that WNS effects on eastern small-footed bats roosting in bridges in summer were minimal since we detected no significant change in overall population numbers during the 8 years of study and annual survival rates were comparable or higher than survival recorded prior to WNS.

Because eastern small-footed bats move frequently (often daily) among rock outcrops and boulder crevices during summer (e.g., Johnson and Gates 2008), long-term monitoring or survival estimates in these habitat structures are difficult, whereas their use of bridges made long-term banding and survival estimates more feasible. Nevertheless, it is unknown if eastern small-footed bats roosting in bridges have survival rates that differ from bats roosting in natural structures such as talus slopes and additional study is needed to determine if roosting in bridges offers costs or benefits over natural roosts such as reduced predation or greater mortality due to vehicular traffic.

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Author Contributions

DBS conceptualization, investigation, writing, review, and editing; RWP formal analysis, writing, review, and editing.

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