TRENDS IN ABUNDANCE OF HIBERNATING BATS IN A KARST REGION OF THE SOUTHERN GREAT PLAINS

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ABSTRACT—We analyzed temporal variation in abundance of hibernating bats from long-term records (1965–2004) in gypsum caves of the Red Hills of Kansas and Oklahoma, a region lying at peripheries of geographic ranges of four species of bats. Nonparametric correlation analyses were used to evaluate variation in abundances of five species among 12 hibernacula. Townsend's big-eared bat (*Corynorhinus townsendii*) showed no significant change in abundance among most of its hibernacula, but exhibited one increase and one decrease in abundance in two hibernacula. The cave myotis (*Myotis velifer*) displayed increasing abundance in some hibernacula (27% of hibernacula, $n = 3$) and one decrease (9% of hibernacula, $n = 1$). The tri-colored bat (*Perimyotis subflavus*) exhibited increasing abundance in 60% ($n = 6$) of its hibernacula. The pallid bat (*Antrozous pallidus*) and big brown bat (*Eptesicus fuscus*) exhibited no statistically significant change in size of population in any hibernaculum, although the pallid bat occurred infrequently and in low numbers (≤11 individuals) in the hibernaculum where it was detected. The changes in abundance we detected may reflect range expansions of some species (e.g., tri-colored bat) or changes in qualities of hibernacula or other aspects of habitats, but underlying mechanisms are unknown.

RESUMEN—Analizamos la variación temporal en abundancia de murciélagos en invernaderos por medio de registros de largo plazo (1965–2004) en cavernas de yeso de las Red Hills de Kansas y Oklahoma, una región que se encuentra en los límites de las distribuciones geográficas de cuatro especies de murciélagos. Se usó el análisis de correlación no paramétrica para evaluar la variación en abundancia de cinco especies entre 12 invernaderos. El murciélago orejas de mula (*Corynorhinus townsendii*) no mostró cambios significativos en abundancia en la mayoría de sus invernaderos, pero exhibió un aumento y una reducción en abundancia en dos invernaderos. El murciélago de la cueva (*Myotis velifer*) mostró aumento en algunos invernaderos (27% de los invernaderos, $n = 3$) y en un sitio una reducción (9% de los invernaderos, $n = 1$). El murciélago *Perimyotis subflavus* exhibió un aumento en abundancia en 60% ($n = 6$) en sus invernaderos. El murciélago pálido (*Antrozous pallidus*) y el gran murciélago marrón (*Eptesicus fuscus*) no exhibieron cambios significativos con respecto al tamaño poblacional en ningún invernadero, aunque el murciélago pálido apareció en baja frecuencia y en bajos números (≤11 individuos) en el invernadero donde fue detectado. Los cambios en abundancia que detectamos pueden reflejar expansiones en la distribución geográfica de algunas especies (por ejemplo, el murciélago *P. subflavus*) o cambios en la calidad de invernadero u otros aspectos de hábitat, pero se desconocen los mecanismos subyacentes.

Changes in abundance are of basic interest in determining statuses of populations in setting priorities for conservation (Groves et al., 1996; Calkins et al., 1999; Peterjohn and Sauer, 1999), and these changes might serve as indicators of environmental change (Croxall et al., 2002). At peripheries of geographic ranges, densities may be lower, less stable, or exhibit abrupt demarcation due to discontinuous environmental variables (Brown, 1984). However, Lomolino and Channell (1995) reported that endangered mammals tend toward persistence at peripheries, rather than at cores, of their geographic ranges. Thus, monitoring across entire geographic ranges provides the most complete perspectives of biogeographic trends in size of populations.

Long-term surveys of populations of bats are of great interest to conservationists (O'Shea et al., 2003), although there is a paucity of such surveys in the literature. Such surveys have been conducted on endangered species in North America, notably for the gray myotis (*Myotis grisescens*) and Indiana myotis (*Myotis sodalis*; Tuttle, 1979; Elliott, 2008), with some surveys providing ancillary information on other species of bats (Whitaker et al., 2002; Brack et al., 2003). In Europe, populations of hibernating bats in mines of the Czech Republic were surveyed for >28 years (Rehak and Gaisler, 1999). The most comprehensive analysis of changes in populations of bats was done by Ellison et al. (2003). As there is no formal survey program encompassing all species of bats across the United States, comprehensive evaluation of populations is available only through compilation of localized surveys (Ellison et al., 2003).

The Southwest Tablelands ecoregion of the southern Great Plains of North America (Fig. 1) contains karst landscapes with numerous caves that provide important roosting sites for cavernicolous bats, especially at its easternmost portion in Kansas and Oklahoma. This area, referred to as the Red Hills, offers critical habitat for some bats at peripheries of their range. In Kansas, some cavernicolous species are restricted to the Red Hills region, including the pallid bat (*Antrozous pallidus*), Townsend's big-eared bat (*Corynorhinus townsendii*), and cave myotis (*Myotis velifer*; Sparks and Choate, 2000). These three species, plus the big brown bat (*Eptesicus fuscus*) and tri-colored bat (formerly known as the eastern pipistrelle; *Perimyotis subflavus*), are non-migratory in this region and use caves as winter hibernacula. Periodic counts of bats wintering in gypsum caves of the Red Hills have been made since 1964, providing a valuable long-term database for assessing changes in resident populations of bats. Here we present an analysis of long-term trends in abundance of hibernating bats among these gypsum caves. The only species we studied that was not at the periphery of its range in the Red Hills is the big brown bat. The pallid bat and Townsend's big-eared bat are listed as species in need of conservation by the Kansas Department of Wildlife and Parks.

Materials and Methods—Hibernacula in karst landscapes of Kansas and Oklahoma were surveyed during 1964–2005. In the 42-years, there was a total of 29 years with surveys and 95 days with observations. Among the 48 hibernacula, one (a natural cave) was located in Oklahoma (Woods County), with the remainder being distributed across Barber and Comanche counties in Kansas. Most hibernacula consisted of gypsum caves, with the exception of one bluff crevice (a roost with pallid bats) and an active gypsum mine. Hibernacula were located across ca. 40-km of latitude in the Red Hills region (Fig. 1). This area is in the mixed-grass prairie of the Great Plains and is characterized by irregularly dissected slopes, bluffs, and gypsum-capped buttes. Eastern red cedars (*Juniperus virginiana*) are common and cattle ranching is the predominant use of land. Hibernacula were on private lands; for security, hibernacula are named with 2–4-letter codes. Humphrey and Kunz (1976) provided a detailed description of the study area.

Caves, mines, and crevices used as hibernacula usually were visited 1 December–1 March. Survey during hibernation minimizes variation in estimates of abundance that might be caused by variable use of roosts during other times of the year (Tuttle, 2003). To minimize disturbance and arousal of hibernating bats, individual hibernacula typically were not surveyed in consecutive years. Due to logistical constraints, only some of the caves could be surveyed each hibernation season and the number of hibernacula sampled varied annually (range, 1–15; mean, 7). Accordingly, analyses of changes in abundance were performed for individual hibernacula.

Within hibernacula, only areas that were consistently available and observable were searched for bats. When solitary bats or small clusters were discovered, individuals were counted. When large clusters were encountered, density within subsamples was estimated and area of cluster was used to estimate abundance (Tuttle, 2003). In an attempt to ensure sampling was consistent among sites and years, all counts were made by one observer (SDR). In a few instances, qualitative estimates of abundance were made and these data were omitted from analyses. As in all surveys of wildlife, sampling error was inevitable; however, sampling error was consistent over time and, thus, estimates of trends should not be biased. Because some bats may have been undetectable, our survey likely underestimated absolute abundance. Although gypsum caves often are unstable (Young and Beard, 1993), those included in our analyses appeared to be structurally stable over the survey period. One cave exhibited considerable changes in structure and was omitted from analyses.

Because hibernation spanned calendar years, we labeled the year of survey with the calendar year when bats entered hibernation. Because varying numbers of caves were sampled each year, changes in size of populations were analyzed separately for each species in each hibernaculum. A similar approach was used by Ellison et al. (2003). In analyses, we included only the 12 hibernacula that were surveyed over a ≥20-year span, those with the last survey completed during 2000 or more recently, and those with ≥5 years of data (Fig. 1). If >1 survey was conducted at a hibernaculum within the same year of survey, we used the maximum number of bats counted that year in analyses.

Data from counts did not meet the normality assumption of linear-regression analysis. We used Spearman-rank correlation (PROC CORR; SAS Institute, Inc., Cary, North Carolina) to analyze changes in abundance among years. Categorical trends of increasing (positive ρ), decreasing (negative ρ), or stable populations (non-significant ρ) were delineated based

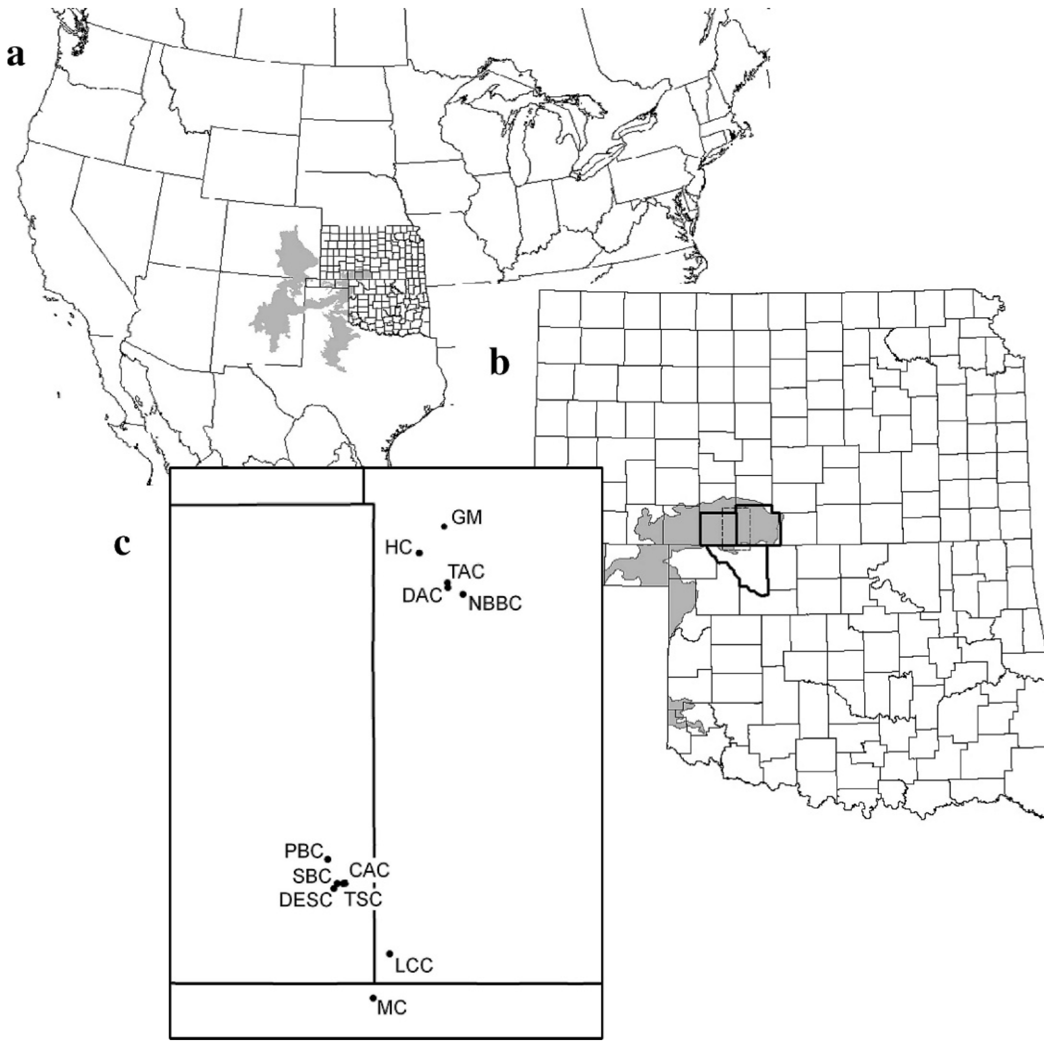

Fig. 1—a) Southwest Tablelands ecoregion (gray) of North America, b) subregion within Kansas and Oklahoma referred to as the Red Hills (modified from United States Environmental Protection Agency), and c) locations of 12 hibernacula in three counties used for analyses of trends in populations of bats.

on α = 0.05, although we use the term tendency in discussing trends with marginally significant *P*-values (above but near 0.05).

Results—There was a total of 134,839 detections of individual bats during 1965–2004 among the 12 hibernacula. Five species of hibernating bats were encountered: pallid bat (n = 28), Townsend's big-eared bat (n = 1,968), big brown bat (n = 901), cave myotis (n = 131,624), and tri-colored bat (n = 318).

Townsend's big-eared bat was found in 10 hibernacula with counts of 0–235 individuals (Figs. 2 and 3). This species exhibited statistically significant change in abundance in only two hibernacula (one increase, one decrease) with a tendency toward an increasing population in another (LCC; Table 1). Analyses included seven hibernacula of the big brown bat, with counts of 0–400 individuals (Figs. 2 and 3), but there was no statistically significant change in abundance of this species in any hibernaculum (Table 1). For the cave myotis, analyses included 11 hibernacula and counts were 0–26,500 individuals (Figs. 2 and 3). This species exhibited

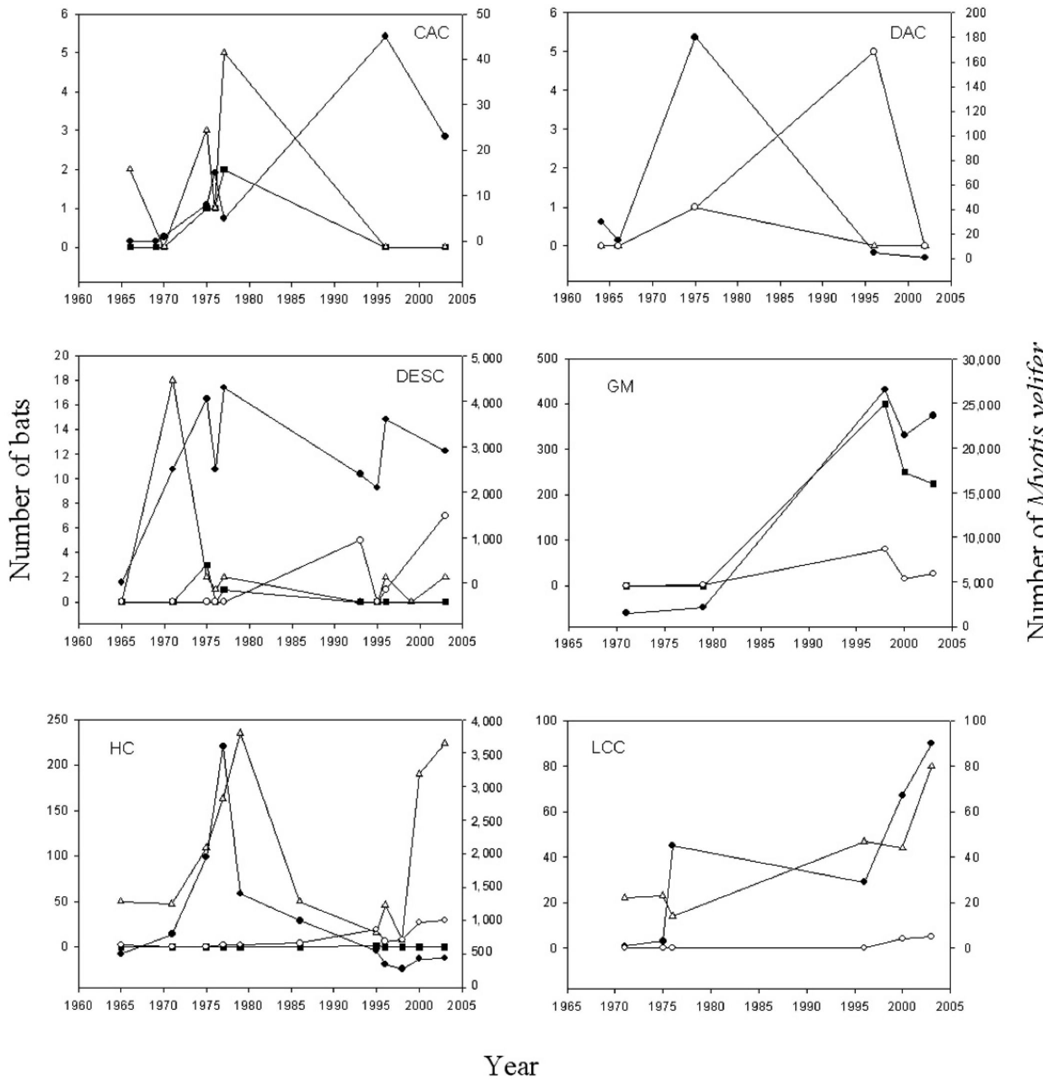

FIG. 2—Variation in abundance of bats in 6 of 12 hibernacula in the Red Hills of Kansas and Oklahoma: open triangles, Townsend's big-eared bat (*Corynorhinus townsendii*); solid squares, big brown bat (*Eptesicus fuscus*); solid circles, cave myotis (*Myotis velifer*; abundance of this species is on right Y-axes); open circles, tri-colored bat (*Perimyotis subflavus*). Origins of Y-axes are negative to illustrate values of zero.

statistically significant changes in abundance in four hibernacula, with three increasing (Table 1). Analyses for the tri-colored bat included 10 hibernacula, counts were 0–80 individuals (Figs. 2 and 3), and statistically significant changes were detected at six hibernacula, all indicating increasing abundance (Table 1). The pallid bat was found at only one hibernaculum (NBBC). This species was observed during 4 of 9 years at this location with counts of 0–11 individuals. The temporal trend in abundance for pallid bats was not statistically significant ($\rho = -0.26$, $P = 0.507$; Fig. 3).

DISCUSSION—The five species of bats hibernating in the Red Hills of Kansas and Oklahoma exhibited variable changes in abundance over the 40 years of surveys. Increasing abundance of bats in some hibernacula might reflect expansions of geographic range, especially for species at the periphery of their range (e.g., cave myotis and tri-colored bat). However, with the excep-

Table 1—Trends in abundance of four species of bats among 11 hibernacula in the Red Hills of Kansas and Oklahoma, 1965–2004. Trends were analyzed using Spearman-rank correlation, from which rho (ρ) statistics and probability values (*P*) are shown for each species and hibernaculum; *n* = number of years that hibernacula were surveyed. Increasing and decreasing trends in abundance are indicated with positive and negative ρ-statistics, respectively. A dash indicates that samples were too small for analysis or that the species was not detected in that hibernaculum.

		Townsend's big-eared bat (*Corynorhinus townsendii*)		Big brown bat (*Eptesicus fuscus*)		Cave myotis (*Myotis velifer*)		Tri-colored bat (*Perimyotis subflavus*)	
Hibernaculum	*n*	ρ	*P*	ρ	*P*	ρ	*P*	ρ	*P*
CAC	8	−0.30	0.519	0.21	0.624	0.90	0.002	—	—
DAC	5	0.00	1.000	—	—	−0.70	0.188	0.33	0.581
DESC	10	−0.13	0.722	−0.23	0.555	0.23	0.544	0.73	0.025
GM	5	—	—	0.56	0.322	0.70	0.188	0.70	0.188
HC	11	0.05	0.884	0.10	0.770	−0.63	0.039	0.92	<0.001
LCC	6	0.77	0.072	—	—	0.94	0.005	0.85	0.034
MC	8	0.79	0.021	−0.05	0.898	−0.30	0.624	0.85	0.008
PBC	8	0.26	0.542	—	—	0.07	0.867	0.52	0.185
SBC	10	−0.59	0.092	−0.41	0.244	0.78	0.008	0.70	0.025
TAC	8	−0.80	0.016	−0.28	0.497	−0.41	0.317	0.94	0.001
TSC	9	0.24	0.526	—	—	0.07	0.865	0.48	0.192

tion of the tri-colored bat, species did not exhibit statistically significant changes in abundance in most hibernacula. This lack of detectable change might be due to variability among years in use of hibernacula or it could reflect consistent availability of resources and other factors. While structural changes in caves or fluctuations in climate can affect use of a hibernaculum (Humphrey and Kunz, 1976; Briggler and Prather, 2003; Johnson et al., 2005; Lausen and Barclay, 2006), no change was observed in caves included in our analyses. However, changes involving caves that were not included in our surveys could have altered overall availability of suitable hibernacula in the study area, affecting immigration of bats to, and emigration from, the caves we surveyed (Lewis, 1995).

Transformation of landscapes, particularly changes in vegetational cover, modifies habitat of bats with regard to avoiding predators (Burford and Lacki, 1995), altering flight patterns (Patriquin and Barclay, 2003), drinking habitats (Downs and Racey, 2006), and determining patterns of use of habitats (Law and Chidel, 2002; Williams et al., 2006). These changes might affect hibernating populations of resident bats. During our survey, the eastern red cedar expanded across prairies of the Red Hills and across the southern Great Plains in general (Briggs et al., 2002; Horncastle et al., 2004). Additionally, invasion of phreatophytic salt cedar (*Tamarix*) in riparian zones (Gaskin and Schaal, 2002) may affect flow of streams and quality of riparian habitats (Sala et al., 1996). It is not known if such environmental changes have affected the changes in abundance detected in our survey.

Parallel trends in abundance among species within a single hibernaculum could indicate generalized responses to environmental variables, whereas opposing trends could indicate species-specific responses to environmental factors or interspecific competition for roosts or prey (Humphrey, 1975). We detected no evidence that interspecific competition was driving changes in abundance. In some hibernacula, similar changes occurred among sympatrically roosting species, but we noted opposite trends in other hibernacula (e.g., cave myotis and tri-colored bat; Table 1).

Townsend's big-eared bat exhibited no substantial change in abundance during our 40-year survey that generally resembles trends for the species elsewhere in the western United States (Ellison et al., 2003). Variation in counts of this species among years might have masked trends among hibernacula. In Arkansas, *C. t. ingens* moved among hibernacula during winter (Clark

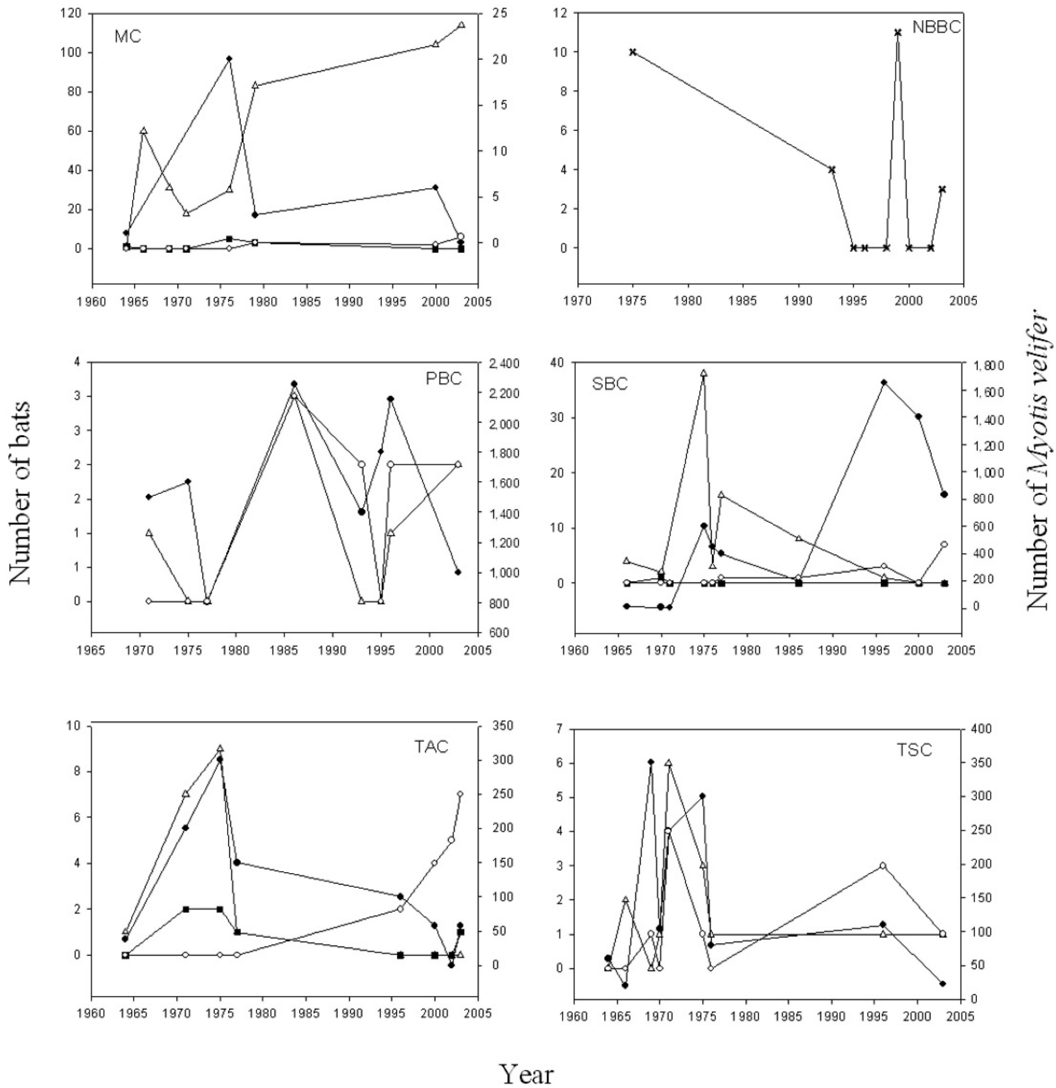

FIG. 3—Variation in abundance of bats in 6 of 12 hibernacula in the Red Hills of Kansas and Oklahoma. Pallid bats (*Antrozous pallidus*; letter x) were only in hibernaculum NBBC. See Fig. 2 for explanation of symbols on graphs.

et al., 2002). Given the conservation status of Townsend's big-eared and pallid bats in Kansas, continued monitoring is warranted. However, it is notable that Townsend's big-eared bat apparently is sensitive to disturbance by humans (Humphrey and Kunz, 1976).

The big brown bat is the only species in our survey for which Kansas and Oklahoma are well within the geographic range; however, the Red Hills region supports the only population of big brown bats in Kansas south and west of the Arkansas River (Sparks and Choate, 2000). Lack of any significant change in abundance of the big brown bat is expected given its wide distribution in North America. In addition to caves, big brown bats use buildings and other structures as hibernacula (Whitaker and Gummer, 1992). Thus, our survey may have underrepresented the big brown bats that hibernate in the Red Hills.

Variation in abundance of cave myotis among hibernacula could reflect local variation in demography or switching of roosts among years. The population of cave myotis in the Red Hills is in the most northeasterly portion of the range of this species. Like some other species we studied, the cave myotis also uses buildings for roosting (Fitch et al., 1981) and has displayed an expansion of its geographic range from the area with a high density of caves in south-central Kansas (Sparks and Choate, 2000). The ability of cave myotis to occupy new roosting habitats might partially explain increases observed in ca. 25% of its hibernacula in the Red Hills. Populations in caves and mines of this region might provide a source for emigration to anthropogenic sites, although this has not been verified.

For the tri-colored bat, there was increasing abundance in >50% of hibernacula and no decrease was detected. In the eastern United States, Ellison et al. (2003) determined that populations were increasing in only 25% of hibernacula. A general expansion of its overall geographic range has occurred (Yancey et al., 1995; Ammerman, 2005; Geluso et al., 2005; White et al., 2006; Kurta et al., 2007), including expansion into the Red Hills (Hibbard, 1934; Twente, 1955; Adams, 1995; Sparks and Choate, 2000). The western periphery of the geographic range is now well into Colorado (Geluso et al., 2005). This expansion is believed to have accompanied westward encroachment of forested habitats in North America (Sparks and Choate, 2000; Geluso et al., 2005); encroachment that has included the southern mixed-grass prairie (Horncastle et al., 2004).

The pallid bat was observed at the only known hibernaculum of the species in Kansas (a bluff crevice), which also is its easternmost occurrence in North America. Although the pallid bat exhibited no statistically significant change in abundance in the Red Hills, individuals were at the site during <50% of the years of surveys. Historically, the species occurred in larger numbers in the Red Hills of Kansas where attempts to eradicate them nearly destroyed a colony of ca. 200 bats in 1964 (Jones et al., 1967; Sparks and Choate, 2000). This species was not detected in the study area for 11 years of our survey (1980–1991) and presumably was extirpated from the state during that period (Sparks and Choate, 2000). Recent records are believed to represent recolonization of the former eastern periphery of its range in Kansas (Sparks and Choate, 2000). In February 2009, 12 pallid bats were in the bluff crevice. Until other roosts of pallid bats are discovered, their conservation status in Kansas remains warranted (Sparks and Choate, 2000).

Standardized surveys of bats should be made across their geographic ranges. O'Shea et al. (2003) cautioned that care should be taken in design of surveys and noted problems inherent to use of indices of abundance for estimating trends in populations. However, alternative methods used to adjust for nuisances in sampling (e.g., undetected individuals) commonly are fraught with unreasonable assumptions (Johnson, 2008). Our investigation provided evidence of changes in size of bat populations in the Red Hills, but we recognize limitations in our methods for accurately estimating abundances of bats. When sampling at roosts, the most accurate estimates likely come from solitarily species or those that roost in small colonies (e.g., <1,000; Kunz, 2003; Tuttle, 2003). In the Red Hills, obtaining accurate estimates of cave myotis was particularly difficult because this species often was roosting in large groups (e.g., >20,000 at one roost). In caves, estimates of density within clusters can be affected by irregularity of substrate and height of ceiling (Kunz, 2003; Tuttle, 2003). Identification of species can be difficult in mixed-species roosts, which may artificially inflate estimates of size of populations for one species while deflating estimates for others (Tuttle, 2003). Size and complexity of caves can limit access by researchers to roosts and result in underestimation of abundance within hibernacula (Tuttle, 2003). Despite these issues, surveys of hibernacula remain standard techniques for estimating changes in abundance of bats, as long as assumptions are recognized and biases are minimized (Tuttle, 2003). If biases are consistent over time, analyses of changes in abundance can be considered valid; we are confident our methods fit this criterion.

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