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Population dynamics and site fidelity of the cave bat, *Myotis velifer*, in Oklahoma

Stephen R. Humphrey* and Madan K. Oli

School of Natural Resources and Environment and Florida Museum of Natural History, University of Florida, 103 Black Hall, Gainesville, FL 32611, USA (SRH)
Department of Wildlife Ecology and Conservation, University of Florida, 110 Newins-Ziegler Hall, Gainesville, FL 32611, USA (MKO)

* *Correspondent: humphrey@ufl.edu*

We characterized population dynamics of nonmigratory cave bats, *Myotis velifer*, in Oklahoma by locating all 21 caves known to be occupied in an exhaustively searched, large study area, marking representative samples with numbered wing bands and conducting annual winter counts and recaptures over a decade. Bats moved readily among maternity caves during summer and among hibernating caves from winter to winter. The aggregate population of adults during lactation was about 13,600, including 10,500 females, of which 96% produced young. The aggregate population during winter was about 23,850 for the first 2 years of the study, declined to about 14,200 in the 3rd year, and recovered to > 20,000 for the last 4 years of the study. Mortality events and threats documented included flooding, subfreezing temperatures, and rock collapses in caves, as well as in-cave disturbance by humans, but the cause of the decline was not identified. We used capture–mark–recapture methods to estimate and model capture probability (P) and apparent survival (ϕ) from 1967–1968 to 1976–1977. Based on bats marked as weaned juveniles at maternity caves, survival was lowest in the first 6 months of age and increased steadily in later age classes. Females survived better than males. Based on subadult and adult bats marked in winter, survival increased over the 1st half of the bats' 10-year life span and then declined over the 2nd half. These results show that survival is strongly sex- and age-specific, with lower survival for juveniles than for older bats and lower survival for males than for females. Site fidelity was relatively weak, apparently enabled by the local abundance and proximity of caves. Rapid recovery from a large population decline indicates substantial resilience in this metapopulation. In contrast, relatively stable numbers in the years before and after the decline suggest that some factor may limit population size under normal conditions.

Key words: capture probability, cave bat, demography, metapopulation, site fidelity, survival rate

Bat species vary widely in their site fidelity (the degree to which they depend on particular sites for crucial life functions—Fisler 1969). Humphrey (1975) hypothesized that highly colonial bats have numerous adaptations associated with use of permanent types of maternity roosts such as caves and buildings, resulting in high survival rates, low natality rates, and low dispersal rates of established adult females. Such demographic attributes are typical of species that have low population growth rates (MacArthur 1969). High site fidelity to permanent roosts appears to offer protection against predators and weather and thermodynamic benefits for bearing and rearing young. To the latter point, Tuttle (1976) documented enhanced survival for young gray bats (*Myotis grisescens*) reared in heat-trapping cave domes. A review by Kunz (1982) confirmed that many colonial bat species have strong site fidelity, with the highest degree found in females during the summer maternity period. Another review restricted to radiotracking studies (Lewis 1995) concluded that bats' site fidelity was related directly to roost permanence and inversely to roost availability. In this paper, we further explore these issues in a cave-dwelling species whose roosts are both permanent and abundant.

Successful demographic studies depend on observable subjects. Among mammals, most bats are secretive, and research on populations has been constrained accordingly. Although obscure bat demography hinders testing hypotheses about mechanisms determining population status and trends, a substantial descriptive literature on bat population dynamics has developed, and valuable reviews have been provided by Tuttle and Stevenson (1982), Keen (1988), and O'Shea et al. (2004). We exploited advantages in field observation to study the population dynamics of the cave bat, *Myotis velifer*, in northwestern Oklahoma. The bats rear young and hibernate in numerous caves formed in horizontal beds of soft gypsum of the Blaine Formation (Fay 1964). The caves develop as small subsurface drainage channels, usually opening downstream as sinkholes or at cliff faces. Their karst topographic features are easily found because the dominant vegetation is mid-grass prairie, with only scattered trees. Maternity colonies occupy the few high, heat-trapping cave domes, and most hibernating bats cluster in monolayers on the "downstream" cave ceilings within reach of researchers. Hibernating bats marked with conventional wing bands are readily visible, enabling researchers to select marked bats for recapture while leaving the unmarked bats hibernating in place. Populations in this part of the species' range are nonmigratory, with most individuals wintering near their maternity sites or up to a few tens of kilometers away (Cockrum 1952; Twente 1955; Tinkle and Patterson 1965). This combination of characteristics favors thorough sampling of the bat populations, especially during winter. We recognized an unusual opportunity to design a mark-and-recapture study consistently in time and space so as to achieve a high recapture rate of marked bats and hence to document annual survival rates relatively accurately.

Our goal was to characterize *M. velifer* populations by documenting population size, movements, and reproduction, while testing for sex- and age-specific differences in annual survival. To achieve the last goal, we applied Cormack–Jolly–Seber modeling methods to capture–mark–recapture data collected during 1967–1977. We expected survival of juvenile bats to be lower than for older bats, and we did not expect a survival difference between the sexes. We delayed analysis of these data long after field work was completed because then-conventional minimum-number-alive methods underestimated true survival rates, while superior Cormack–Jolly–Seber methods were in development at the time field work was completed (Keen 1988; Williams et al. 2002).

MATERIALS AND METHODS

Study area and species.—We systematically located caves and sampled, marked, and recaptured bats in a 31 by 6 km "core study area" along and above the Blaine Formation escarpments south of the Cimarron River, in Major and Woodward Counties, Oklahoma. This study area spanned the southeastern terminus of the exposed, cave-bearing gypsum formation. We did not search systematically for caves farther northwest in Woodward County, but we did sample bats in 2 important caves there. We also sampled bats at caves to the north in Woods County, Oklahoma, and in Comanche and Barber Counties, Kansas, as well as south in Washita County, Oklahoma.

Individual cave populations of *M. velifer* typically number 2,000–5,000 (Fitch et al. 1981), although much larger populations occasionally occur (see "Results"). Females reproduce during their 1st year of life (Kunz 1973) and produce a single young at the age of 1 year (Fitch et al. 1981). The sex ratio of fetuses does not differ from unity (Kunz 1973). Some males may not reproduce until their 2nd year (Krutzsch 1961). Production of sperm begins in early autumn and most copulation occurs in September and October, although some mating occurs during winter (Kunz 1973). In northwestern Texas, *M. velifer* hibernate from mid-October to mid-March (Tinkle and Patterson 1965). In northwestern Oklahoma and southwestern Kansas, they move from hibernation sites to spring roosts or maternity sites in late March and early April (Twente 1955). Ovulation probably occurs when females leave hibernation (Fitch et al. 1981). Young in Oklahoma were reported in the last week of June (Glass and Ward 1959). Kunz (1973) reported that most young in southwestern Kansas are born in the last 2 weeks of June, lactation occurs from mid-June to mid-August, young begin flying in mid-July and are weaned at an age of approximately 6 weeks, and some adult females cease lactating as early as the beginning of August. Most *M. velifer* wintering in northwestern Texas are less than 3 years old (Tinkle and Patterson 1965).

Field methods.—We searched the core study area by vehicle and on foot and located 21 caves occupied by *M. velifer*: 20 used as hibernacula and 3 (including 2 of the former) used as maternity roosts. We were confident that we found all occupied caves in the core area, but this took several years; we located 6 (including the 5 largest populations) in winter 1967–1968, 18 by 1968–1969, 20 by 1969–1970, and the last 1 in 1973–1974. We sampled the maternity populations approximately every 2 weeks during the late pregnancy, lactation, and postlactation season of 1968, until young of the year could no longer be differentiated from adults. These July–August samples were intended to characterize populations and mark individuals for long-term recapture; we marked 3,230 adult and juvenile bats during these samples, or 13.6% of the total population estimated to occupy the core study area in late summer (see "Results"). Because recaptures of marked bats during this summer sampling were only 0.6% of the total population, little documentation of within-summer movement was anticipated. We also sampled and marked bats in the 3 largest hibernating populations in the winter of 1967–1968 and sought to visit all known hibernating populations to make population counts and to recapture marked individuals once per year during winters of 1968–1969 through 1976–1977. We marked 4,489 bats in these winter samples, 18.8% of the total population estimated to occupy the core study area in winter (see "Results"). In contrast to summer, winter recapture effort approached census levels, and we expected to document long-term movements and survival effectively. We also visited hibernacula beyond the study area, to the northwest, north, and south, to recapture marked bats during some years, but visited only one of these (Alabaster Cavern) in all 10 winters. Additional *M. velifer* were captured and marked during summer 1967, during winters after 1967–1968, and in other caves beyond the core study area, but their sample sizes and results are not reported because their sampling design was not optimal.

Challenges of search and commuting time resulted in some missing values in the winter population counts in the core study area. To assess total population size and trend, we adjusted the aggregate number to account for small populations that were not visited in some years, using each cave's average count for years visited. The adjustment was 7,079 bats in 1967–1968, when only 2 of the "other core area caves" had been found; 14 had been found in 1968–1969, 16 in 1969–1970, and all 17 in 1973–1974. The annual adjustment for "other core area caves" in the remaining 9 years averaged 2,806 bats. The smallest per-cave adjustments were 8 bats at Simmons Cave and 13 at Moonshine Cave, which were only visited once because of their small numbers and inaccessibility. The largest per-cave adjustment was 1,960 bats at Switchback Cave, which was not found until 1973–1974.

We evaluated maternity population size during summer by making evening flight counts at cave entrances (Venables 1943; Dwyer 1966; Humphrey and Cope 1970; Kunz 1973), with 2 observers counting simultaneously at Vickery Cave, which had 2 entrances. Bats were counted individually while rates of emergence were low; when rates of emergence were high, bats were counted in groups of 10. Units of 10 were recorded with a mechanical 4-digit tally counter. Because some individuals may have been missed or double-counted, these flight counts were approximate and used as indices of actual population size. Usually we conducted a flight count 1 day before taking a population sample, enabling us to link the sample data to concurrent population size. During winter, visual population counts and sampling to mark or recapture bats were done simultaneously. Summer and winter counts were approximations by experienced observers, but we had no way of estimating detection probability so these counts are indices of abundance rather than accurate counts.

We avoided entering or sampling in the maternity roosts during the summer to avoid disrupting the populations; based on a single exception in July 1967 (see "Results"), we found *M. velifer* to be much more sensitive to nursery disturbance than other *Myotis* species we had studied. Instead, summer samples were taken with hoop-nets at the cave entrances during evening bat flights. Reproductive condition of adult females (latter stage of pregnancy, lactating, postlactating) was determined by palpation of the fetus and examination of the teats (pendulous nipples, reduced fur coverage, white tissue beneath the skin, milk extrudable). Adult females that appeared to be nonreproductive on sample dates when most females were pregnant or lactating were judged to be nonreproducing or to have aborted. Young were distinguished from adults by examination of the phalangeal epiphyses and of the nonpendulous teats of young females (compared with postlactating adults) and the small testes of young males. These age criteria were reliable for all individuals through the 3rd week of August, but in later samples we could not reliably determine age of all bats. Bats were marked with numbered, lipped, size 2b aluminum bat bands (U.S. Fish and Wildlife Service, Washington, D.C.). Because young were not banded until they were captured during evening flights, it was not possible to measure rates of survival between birth and weaning. Summer sample data on sex, age, and reproductive condition were analyzed for each sample, but for survival analysis the biweekly samples were added together to provide a larger breeding season sample for each maternity population.

This research did not follow American Society of Mammalogists guidelines nor was it approved by an institutional animal care and use committee because no such entities existed at the time of data collection.

Samples used for analysis.—For the purpose of analyzing movements and survival, we used samples marked in summer 1968 (prior to the 3rd week of August, when some juveniles became indistinguishable from adults) and in winter 1967–1968. Marked bats were sought for recapture every winter through 1976–1977 systematically within and selectively beyond the core study area. Bats sampled at maternity sites (Vickery, Simmons, Canyon) were combined to increase sample size, and this composite summer sample was divided into juveniles (1–2 months old) and adults ($\geq$ 1 year old). Only individuals marked as juveniles were used for age-specific survival analysis. To examine longer-term trends in survival based on a larger sample but lacking age-specific detail, bats sampled at hibernacula (Goranflo, Inman's, Vickery) during winter 1967–1968 also were combined to form a composite sample. These bats were $\geq$ 0.5 year old. Because the main focus of movement and survival analyses was on long-term patterns and the relationship of summer and winter roosting sites, recaptures made < 6 months after marking were deleted prior to these data analyses. However, we also recorded short-term movements of bats marked and recaptured within summer 1968. For the purpose of analyzing sex ratio, samples at hibernacula in the core area were considered for the 1st year, 1967–1968, for which the aggregate sample was largest.

Capture–mark–recapture analyses.—Of 1,041 juvenile bats sampled, 1,020 were marked and released during summer 1968 at 3 maternity caves in the core study area (Canyon, Simmons, and Vickery). We used the cohort-based mark-recapture modeling framework to estimate age-specific apparent survival rates (Loery et al. 1987; Williams et al. 2002). We only used bats captured, marked, and released as juveniles; consequently, we knew their exact ages when they were subsequently recaptured. We considered 4 age classes: age class 1 ($\leq$ 0.5 year), age class 2 (0.5–1.5 years), age class 3 (1.5–2.5 years), and age class 4 (> 2.5 years old), and we used a sequential approach to the modeling process (Goswami et al. 2011; Loughry et al. 2013). First, we determined an appropriate model structure for the capture probability, *P*. To do so, we allowed apparent survival probability (ϕ) to be time-specific and allowed *P* to be affected by age, sex, location of capture, and additive and interactive (2-way interactions only) effects of these variables. The resulting models for *P* were compared using an information-theoretic approach based on the Akaike Information Criterion corrected for small sample size (AIC_c—Burnham and Anderson 2002) to identify the most parsimonious model structure for *P*. The model with the lowest AIC_c was considered the most parsimonious or best model; models that differed from each other by $\Delta AIC_c \leq 2$ were considered to be well supported by the data (Burnham and Anderson 2002). Next, we fixed model structure for *P* to the most parsimonious model from preceding analyses and allowed ϕ to be affected by the aforementioned covariates and their additive and interactive effects. Again, we used an information-theoretic approach using AIC_c for model comparison and statistical inference.

Our 2nd data set included 4,597 bats $\geq$ 6 months of age that were marked (or recaptured from summer 1967 banding) and released during winter of 1967–1968 in the 3 largest wintering populations (Goranflo, Inman's, and Vickery) in the core study area. We used the Cormack–Jolly–Seber modeling framework to estimate and model ϕ. The analytical approach was identical to that used for known-age bats, except that effect of age was not considered because exact age of these bats was not known.

All capture–mark–recapture analyses were performed in program MARK (White and Burnham 1999) version 6.2 implemented using the RMark package for program R (Laake and Rexstad 2014) version 2.15.2. The goodness of fit test implemented in RELEASE test 2 + 3 did not reveal lack of fit or overdispersion of data for the known-age data set ($\chi^2 = 11.32$, *d.f.* = 19, $\hat{c} = 0.596$, $P = 0.910$). However, goodness of fit revealed overdispersion of unknown-age data ($\chi^2 = 105.78$, *d.f.* = 62, $\hat{c} = 0.596$, $P = 0.004$). Consequently, quasilikelihood adjustments were made using the estimated value of $\hat{c}$ (Williams et al. 2002).

RESULTS

Movements.—Bats readily moved among the 3 maternity caves during summer 1968; 8 adults and 3 juveniles moved from one cave to another, out of a total of 137 recaptures during this period. Most longer-term movements among caves also were within the core area. Considering bats marked as juveniles and recaptured in winter, 90.0% of 300 recaptures of 200 unique individuals were at core area caves, 6.7% were approximately 40 km to the northwest at Selman Cave or Alabaster Cave in Woodward County, Oklahoma, 2.7% were approximately 45 km to the north at caves in Woods County, Oklahoma, or 75 km to the north in Comanche and Barber Counties, Kansas, and 0.7% were from noncave locations. Considering adult bats marked in summer and recaptured in winter, 81.4% of 830 recaptures of 559 unique individuals were at core area caves, 17.8% were to the northwest at Selman–Alabaster in Woodward County, Oklahoma, 0.5% were to the north at caves in Woods County, Oklahoma, and Comanche and Barber Counties, Kansas, and 0.2% were from noncave locations. Considering the unknown-age bats marked in winter, 99.5% of 3,165 recaptures of 1,552 unique individuals were at core area caves, 0.2% were to the northwest at Selman–Alabaster in Woodward County, Oklahoma, 0.1% were to the north at caves in Woods County, Oklahoma, and Comanche and Barber Counties, Kansas, 0.1% were from noncave locations, and 0.1% were approximately 110 km to the south at Washita Bat Cave in Washita County, Oklahoma.

Summer population dynamics.—Numbers of bats in maternity caves and sex composition changed during summer, shown by flight counts, sample data, and movement records. During pregnancy (May and June), Vickery Cave housed the largest population, and 63% of these adults were females (Table 1). During lactation and after weaning (late July to mid-August), many of these bats moved from Vickery to Canyon and

Table 1.—Flight counts and number of bats sampled (*n*) in summer maternity populations of *Myotis velifer* in the core study area, Oklahoma. Samples include recaptures of previously marked individuals. Because particular sampling dates differed among locations, data are grouped within seasonal events with date intervals formatted as the beginning year, month, and day followed by the ending (month and) day.

Site Seasonal events	Date	Flight count	*n*	% females among adults	Juveniles in sample	% females among juveniles
Vickery Cave						
Pregnancy	1968.05.12-06.06	5,500	286	63		
Pregnancy/lactation	1968.06.24-26	7,420	200	58		
Lactation	1968.07.04-10	4,896	116	91	0	
Lactation/weaning	1968.07.18-29	5,615	150	88	54	52
Postlactation	1968.08.11-21	5,508	829	84	395	47
Simmons Cave						
Pregnancy	1968.05.12-06.06	605	0			
Pregnancy/lactation	1968.06.24-26	976	284	87		
Lactation	1968.07.04-10	7,179	166	81	0	
Lactation/weaning	1968.07.18-29	6,048	449	80	77	51
Postlactation	1968.08.11-21	3,700	316	100	288	46
Canyon Cave						
Pregnancy	1968.05.12-06.06		0			
Pregnancy/lactation	1968.06.24-26	200	0			
Lactation	1968.07.04-10	1,533	138	16		
Lactation/weaning	1968.07.18-29	2,920	142	23	0	
Postlactation	1968.08.11-21	4,620	402	37	226	42
All core area caves						
Pregnancy	1968.05.12-06.06	6,105	0			
Pregnancy/lactation	1968.06.24-26	8,596	484	75		
Lactation	1968.07.04-10	13,608	420	62	0	
Lactation/weaning	1968.07.18-29	14,583	741	68	131	52
Postlactation	1968.08.11-21	13,828	1,547	72	909	46

Simmons Caves. The adult sexes segregated somewhat in the process; during lactation (early and late July), the proportion of adult females at Vickery Cave rose to about 90%, whereas about 80% of adults at Simmons Cave were females and only about 20% at Canyon Cave were females. Although Canyon Cave was considered a maternity cave, its population was small during pregnancy, and most bats there in July and August appeared to have moved from Vickery and Simmons Caves. Among juveniles marked in the core area when 1–2 months old, 46% were female (*n* = 1,020).

The total population of the core area (Table 1) increased during pregnancy (May and June), indicating ongoing arrival of adults from elsewhere. During lactation (early July), the aggregate population was about 13,600 adults, including about 10,500 females. During lactation and lactation/weaning (early and late July), 96% of the adult females sampled (*n* = 677) had reproduced. When newly flying juveniles joined the flight counts and samples (after mid-August), the aggregate population did not increase appreciably, indicating rapid dispersal of bats from the maternity caves.

Winter population dynamics.—During winter, the aggregate population of the core study area (adjusted for missing values) was approximately 23,850 bats for the first 2 years (Fig. 1; Supporting Information S1). A decline to about 14,200 occurred in the 3rd year. Then, the population grew for 4 years (mean annual rate = 12.5%, range 8–20). Finally, the aggregate population stabilized at > 20,000 for the remainder of the study. Individual patterns at the 4 largest core area hibernating populations were idiosyncratic, with only the Goranflo Cave population tracking the overall trend. The trend at Alabaster and Selman Caves, outside the core area, followed a pattern similar to that of the core study area, however, indicating a geographically extensive cause of the decline and recovery. Sex ratios of hibernating populations were quite variable among samples, sites, and years (Supporting Information S1), with an aggregate value of 56% female in 1967–1968 (*n* = 4,597).

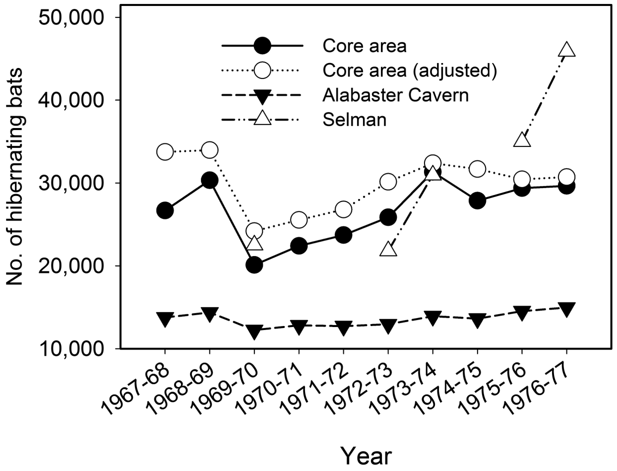

Fig. 1.—Number of *Myotis velifer* counted in various caves in Major and Woodward Counties, Oklahoma, United States, during winters 1967–1968 to 1976–1977. “Core area” refers to aggregate raw counts; “Core area adjusted” refers to aggregate counts adjusted for missing values in some years (see “Materials and Methods”).

Mortality events and threats.—Numerous mortality events and threats were documented, including cave flooding, subfreezing temperatures, rock collapses, and disturbances by people. Evidence of recent flooding was noted in several caves (Vickery, Harmon, Pigpen, Mud, and Selenite) in the winter of 1968–1969, including fresh sediment deposits, deep mud, and high water marks and detritus (to the ceiling in Harmon and Selenite). A landowner reported that this flooding was caused by heavy rain in August 1968. These caves are distributed across a geographic area of 3 × 3 km. In the winter of 1969–1970, we observed a new high water mark 4 m above the floor of Pigpen Cave. In the winter of 1970–1971, the previously muddy Harmon and Mud Caves were very dry. In the winter of 1973–1974, we noted new evidence of flooding in Vickery, Goranflo, Harmon, Pigpen, Mud, Inman’s, Selenite, and Cow Caves, spanning a larger area, 3 × 8 km. Two landowners reported that heavy rains had fallen in late August and early September 1973. The latter 6 (smaller) caves had high water marks and detritus to the ceiling in the entire cave (in 1) or the downstream portion (in 5).

Cold temperatures in caves were occasionally implicated in observed threats or deaths of hibernating bats. Most bats wintering in Vickery Cave normally roosted in a 1-km-long segment of the cave providing a wide array of relatively stable winter temperatures. On 5 December 1972, we observed a large hibernating cluster of 2,200 *M. velifer*, located in a seldom-occupied, short (0.4 km), well-ventilated segment of the cave, in the process of arousing and moving in response to a strong breeze of subfreezing air, hours after passage of a severe cold weather front. On 9 January 1974, we observed dead bats in the coldest portions of this Vickery Cave segment. The next day, in Pigpen Cave, we found 34 dead and dying *M. velifer* that had fallen into the water below from a cold ceiling near the entrance.

Collapsing rock killed bats on at least 1 occasion. On 26 January 1972, we found a section of rock that had recently fallen from the ceiling of Canyon Cave, and we recovered 447 dead *M. velifer*, part of a larger cluster that was crushed and buried under this slab. On 2 December 1974, we found a large section (1 × 6 × 10 m) of the ceiling that had fallen to the floor of Hathaway Cave; whether any bats were present when this fell is unknown.

We found evidence that disturbance of bats in their maternity roosts caused abandonment. At the beginning of the study, on 26 July 1967, we entered the dome of Simmons Cave housing the maternity population of approximately 3,000 bats; some of the young were flightless at that time. Most individuals flew immediately when we entered. We observed the bats for 5 min with flashlights and left the cave. A month later, on 26 August 1967, all bats were absent from Simmons Cave. This observation led us to avoid disturbing maternity roosts for the remainder of the study.

Groups of spelunkers reported traversing the dome of Vickery Cave occupied by the maternity roost on 26 July and 20 September 1969; some juveniles would have been flightless on the former date. Our 1969 evening flight counts at the

Vickery Cave entrances recorded a rapid population decline after the 1st of these dates, from 3,504 on 15 July and 3,630 on 27 July to 1,734 on 3 August, to 1,279 on 9 August, and 791 on 15 August. Fall swarming (aggregation for breeding) brought a population increase to 2,032 on 29 August, 4,501 on 6 September, and 7,114 on 20 September. But on 26 September, the population had dropped to 1,890 bats. This decline was not accompanied by a major weather change. The 1969 counts contrasted with our 1st count of 24,259 bats at Vickery Cave during fall swarming on 15 September 1967.

Much more frequent but indirect disturbance occurred at Alabaster Cavern State Park, which for many years has had multiple daily guided tours through the cave and a circuit of incandescent lights turned on while tourists were present. Maternity and hibernating roost sites of *M. velifer* were located near but not within sight of the tourist path, and the continuity of these populations indicated little effect of the people and lights. When the 150 Watt light fixture in a dome used as the maternity roost disintegrated in 1973, the bats moved to an adjacent dome whose lights continued to function.

Survival of known-age bats.—Searching for recaptures of bats marked as juveniles resulted in 164 recaptures. The number of bats recaptured each winter declined steadily over time. The decline was sharpest in the first 6 months of age for juvenile bats marked during summer (Fig. 2A). Sex ratio of marked and subsequently recaptured bats did not deviate from parity throughout the study period.

For bats marked as juveniles, the most parsimonious model for capture probability (P) included an additive effect of age and capture site (Table 2A; Supporting Information S2). However, another well-supported model ($\Delta AIC_c = 1.06$) suggested that P varied among capture sites (caves), suggesting that age-specific variation in P was insubstantial. We used the latter model for subsequent analysis because it was well supported by data. Based on this model, P was highest for Canyon Cave and lowest for Simmons Cave (Fig. 3A).

The best model for apparent survival (ϕ) included an additive effect of age and sex, suggesting age- and sex-specific variation in survival. Based on this model, survival was lowest for age class 1 (the 6-month interval from weaning to mid-winter) and increased steadily for older age classes. Moreover, females had higher survival than males for all age classes (Fig. 4A). The 2nd best model added an effect of capture site, indicating that individual nursery caves influenced both apparent survival and capture probability.

Survival of unknown-age bats.—Searching for recaptures of bats marked as adults resulted in 7,825 recaptures. Like the known-age bats, the number of unknown-age bats recaptured each winter declined steadily over time, and the decline was the sharpest during the 1st year (Fig. 2B). Sex ratio of marked and subsequently recaptured bats was slightly female-biased during most of the study.

The most parsimonious model for P that could be fit to our data included an interactive effect of sex and capture site (cave). Based on this model, P was highest for Inman's Cave, lowest for Simmons Cave, and higher for females than males (Fig. 3B).

The most parsimonious model for ϕ included an additive effect of time and sex; this model carried virtually all model weight (Table 2B). Time-specific survival for bats of unknown age was low during the 1st year of the study, increased through winter 1971–1972, and subsequently declined (Fig. 4B). This chronological pattern of increasing and decreasing survival was interrupted by a sharp dip in survival recorded in winter 1970–1971. Females had higher survival than males for all years of the study, but the trends over time were similar for both sexes.

DISCUSSION

Number and movement of bats.—*Myotis velifer* depended strongly on numerous caves within and beyond the core study area, but these were not discrete, isolated populations, and fidelity to individual sites was relatively weak, consistent with the effects of roost permanence and availability summarized by Lewis (1995). Movements showed that the entire area sampled, extending approximately 53 km from southeast to northwest and 186 km from north to south, contained a single metapopulation (Levins 1969; Hanski 1999). Bats moved readily among core area caves and to a lesser extent among more distant caves.

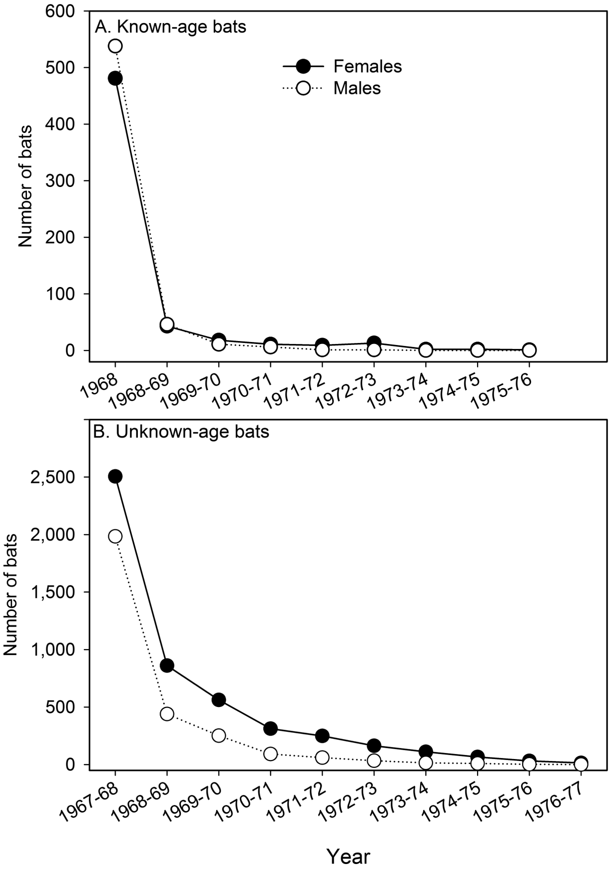

Fig. 2.—A) Number of bats marked as weaned juveniles in summer 1968 that were subsequently recaptured in winters through 1976–1977. B) Number of captures or recaptures of bats ≥ 6 months of age sampled during winters of 1968–1969 to 1976–1977. Note that these numbers also include bats from (A) that survived to ≥ 6 months of age (they were included in the sample with their 1st recapture treated as the date of marking).

Table 2.—A) Models of apparent postweaning survival of known-age cohorts, compared to test for effects of age (age class 1: ≤ 0.5 year; age class 2: 0.5–1.5 years; age class 3: 1.5–2.5 years; and age class 4: > 2.5 years), sex, capture sites (Canyon, Simmons, and Vickery), time (year of sampling), temporal trend (time), and additive and interactive effects of these variables on apparent survival (ϕ). Bats were captured and marked as juveniles in nursery caves. Variables presented are number of parameters (*k*), Akaike Information Criterion corrected for small sample size (AIC_c), differences in AIC_c between the best model and each model in the set (ΔAIC_c), and Akaike weights (Burnham and Anderson 2002). For these analyses, capture probability was modeled as {*P*(cap_site)}. B) Models of apparent survival of unknown-age cohorts (marked in winter, individuals ≥ 6 months of age), compared to test for effects of sex, capture sites (Canyon, Goranflo, Inman, and Vickery), time (year of sampling), temporal trend (Time), and additive and interactive effects of these variables on ϕ. Variables presented are as in (A). Capture probability was modeled as {*P*(sex * cap_site)} (Supporting Information S2, Table S2A). A "+" indicates an additive effect, a "*" indicates an interactive effect, and a "." indicates a constant parameter model.

A) Known-age bats

Model	*k*	AIC_c	ΔAIC_c	Weight
ϕ(age + sex)	10	1,132.195	0.000	0.545
ϕ(cap_site + age + sex)	12	1,134.277	2.082	0.192
ϕ(age * sex)	13	1,135.077	2.882	0.129
ϕ(cap_site + age * sex)	15	1,136.893	4.697	0.052
ϕ(time)	13	1,138.327	6.132	0.025
ϕ(age)	9	1,139.160	6.965	0.017
ϕ(cap_site * age + sex)	18	1,139.602	7.407	0.013
ϕ(time + cap_site)	15	1,139.990	7.795	0.011
ϕ(time * sex)	21	1,140.469	8.274	0.009
ϕ(cap_site + age)	11	1,141.231	9.036	0.006
ϕ(cap_site * age)	17	1,146.026	13.831	0.001
ϕ(cap_site * age * sex)	29	1,148.189	15.994	0.000
ϕ(time * cap_site)	29	1,156.710	24.515	0.000
ϕ(Time * sex)	9	1,170.091	37.896	0.000
ϕ(Time)	7	1,175.804	43.609	0.000
ϕ(cap_site * sex)	11	1,189.433	57.238	0.000
ϕ(sex)	7	1,190.850	58.655	0.000
ϕ(cap_site + sex)	9	1,192.225	60.030	0.000
ϕ(.)	6	1,204.814	72.619	0.000
ϕ(cap_site)	8	1,205.880	73.685	0.000

B) Bats ≥ 6 months of age

Model	*k*	QAIC_c	ΔQAIC_c	Weight
ϕ(time + sex)	16	8,187.254	0.0	0.999
ϕ(time * sex)	24	8,201.102	13.848	0.001
ϕ(Time * sex)	10	8,219.843	32.859	0.000
ϕ(sex)	9	8,219.960	32.706	0.000
ϕ(Time + sex)	8	8,242.612	55.358	0.000
ϕ(sex + cap_site)	12	8,243.022	55.768	0.000
ϕ(sex * cap_site)	16	8,246.416	59.162	0.000
ϕ(time + cap_site)	19	8,290.518	103.264	0.000
ϕ(time)	15	8,295.919	112.616	0.000
ϕ(Time)	8	8,323.020	139.717	0.000
ϕ(time * cap_site)	51	8,326.128	138.874	0.000
ϕ(.)	7	8,353.411	166.157	0.000
ϕ(cap_site)	11	8,354.648	167.394	0.000

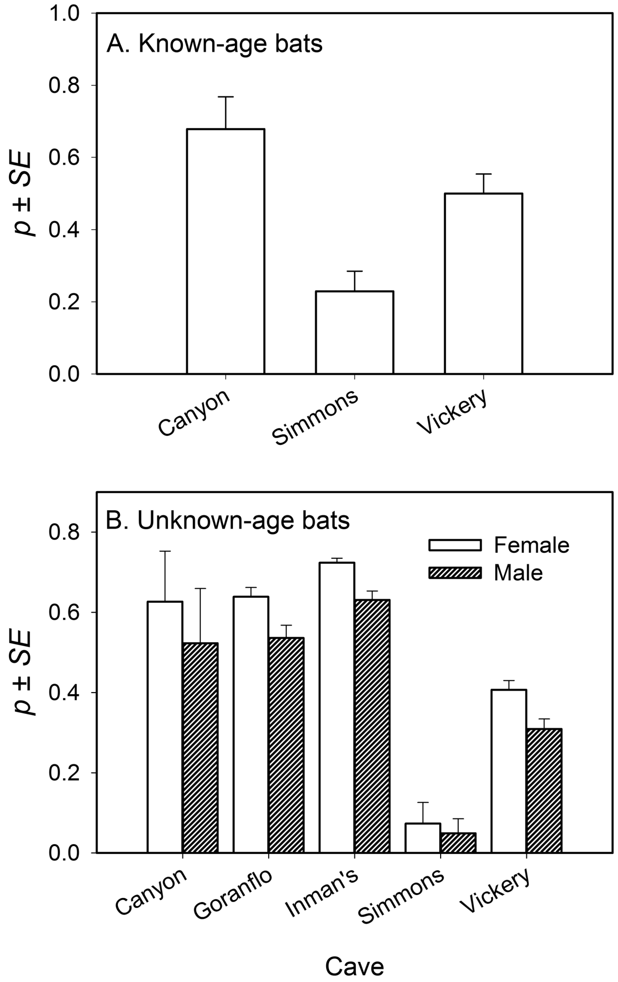

Fig. 3.—A) Capture probabilities (*P* ± *SE*) for known-aged bats that were marked as weaned juveniles in summer 1968. Capture probabilities were estimated using the 2nd model in Table 2A. B) Capture probabilities for unknown-age bats (≥ 6 months old), estimated using the 2nd model in Table 2B.

Trends of counts at the maternity populations during summer did not conform to the simple dynamics to be expected if bats had used roosts in isolation (e.g., Humphrey and Cope 1976; figures 10–11). First, total number of adults increased substantially during pregnancy and lactation rather than remaining stable; late arrivals could have come from other caves outside the core study area, or from other roosts not examined by this study, such as buildings (Kunz 1973). Second, total number of bats did not increase by the approximate number weaned because bats did not stay at the primary maternity site, Vickery Cave, for the entire process of reproduction. After spelunkers traversed Vickery Cave in July and September 1968, large numbers of pregnant or lactating bats apparently moved, completing reproduction at Simmons and Canyon Caves. This ability to move in summer enabled the bats to shift to potentially more secure locations when roost sites were disturbed. Similarly, movement among sites in other seasons enabled bats to respond to threats of flooding and freezing. Access to numerous roosts therefore should tend to ensure

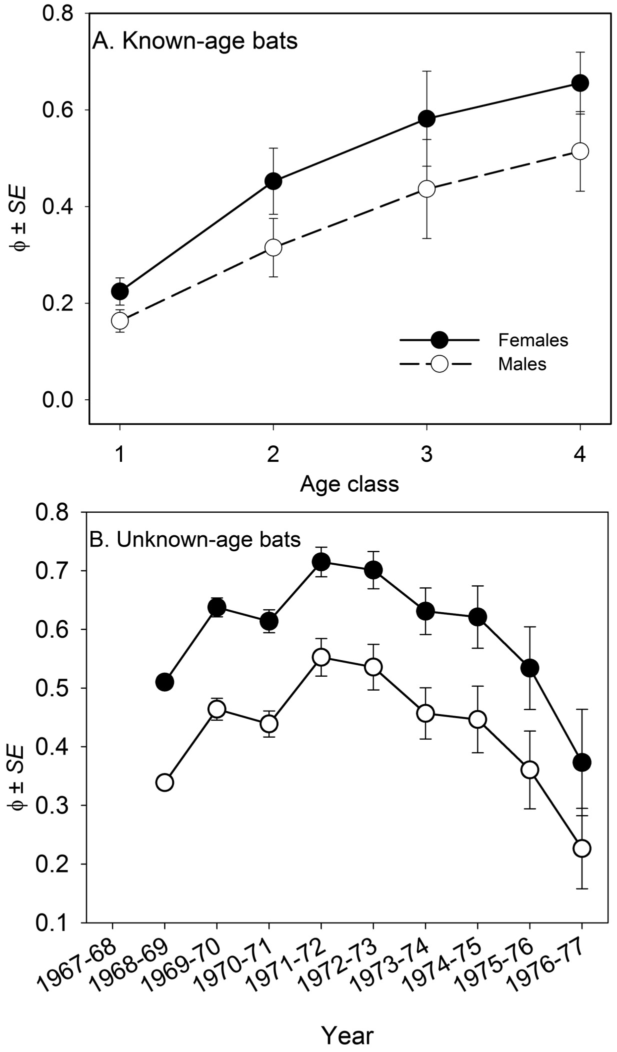

Fig. 4.—A) Age-specific apparent survival probabilities (ϕ ± *SE*) based on known-age bats marked as weaned juveniles in summer 1968. These estimates are based on the most parsimonious model in Supporting Information S2 (Table S2A) that estimated all parameters (i.e., ϕ(age + sex)). Age classes are: age class 1: ≤ 0.5 year; age class 2: 0.5–1.5 years; age class 3: 1.5–2.5 years; and age class 4: > 2.5 years of age. Note that survival of age class 1 is 6-month survival. B) Year-specific apparent survival probabilities for unknown-age bats (≥ 6 months old), estimated based on model {ϕ(time + sex)} in Supporting Information S2 (Table S2A).

long-term survival of the overall *M. velifer* population despite threats and mortality events at individual locations.

The mobility of bats connecting occupied sites during summer made it difficult to understand the dynamics of these populations when examined individually. Instead, observing multiple sites on a substantial geographic scale (the core study area) provided a more comprehensive and meaningful view. Based on the July flight counts and samples at all 3 maternity sites, about 10,100 young were calculated to have been born in the core area (Supporting Information S3). The number of adults counted and the calculated number of births indicate a total of about 23,700 individuals at the population peak in July 1968.

Total population during the winters of 1967–1968 and 1968–1969 in the 21 occupied core area caves (about 23,850) was similar to that of the 3 core area caves occupied in summer 1968. Concordance of the summer and winter estimates appears to confirm that working at an aggregate scale rather than studying individual caves was necessary to understand population dynamics.

Trend in core area winter population size over a decade showed consistent numbers for the first 2 years and then a 40% decline in 1969–1970. The decline was corroborated at a regional scale (40 km to the northwest) by a 35% decline at Alabaster Cavern and by a low count (relative to counts in subsequent years) at Selman Cave. Over the subsequent 4 years the core area population recovered to its initial numbers, as did the Alabaster Cavern population; the Selman Cave population also rose synchronously.

The geographic scale of this decline and recovery indicates a regional cause, such as weather or disease, rather than local events such as a rockfall or human disturbance. Although we documented several categories, events, and threats of mass mortality, we did not identify the cause of the 1969 decline. Cave flooding during the reported heavy August 1968 rains, implicated by signs of high water observed in caves we visited in winter 1969–1970, was the most likely cause, but we did not monitor cave hydrogeology or the maternity roosts within caves. High-rainfall events were recorded in July, August, October, and November 1968 at the 3 National Oceanographic and Atmospheric Agency weather stations nearest the core study area (distances of 40–57 km, Freedom, Dacoma, and Oakwood, Oklahoma—National Oceanographic and Atmospheric Administration 2013), but lack of concordance indicates that these were localized events, so their relation to conditions in the study area caves is unclear. Furthermore, the even more extensive signs of cave flooding found in winter 1973–1974, also attributed to heavy rain in the prior August–September, was not accompanied by a 2nd decline in bat populations. Another possible cause of the decline is our research activity, but we interpret its timing as inconsistent with this explanation. Our netting at summer roosts ceased in 1968; had that been deleterious, we would have expected to record a decline in winter 1968–1969 compared with the previous winter. Similarly, our winter sampling in the core area caves peaked in the 1st year of field work and declined thereafter, totaling about 4,500 bats captured in winter 1967–1968 and 1,200 in winter 1968–1969; had this been deleterious, we would have expected to record an effect beginning in winter 1968–1969 rather than a year later.

The overall winter estimates of bats hibernating in the core area indicate that 2 discrete population phases occurred during the study. The population grew rapidly for 4 years after the large decline recorded in 1970–1971; we infer that the population had ample resources and demographic vigor enabling this recovery. In contrast, the population was relatively stable for the 2 years before the decline and the 4 years after the recovery; we infer that some factor was limiting at the level of 20,000–24,000 bats. We do not know what caused the decline or what may limit the population. A study at a smaller spatial scale and duration would not have been sufficient to identify these major population dynamics.

Capture probability and apparent survival.—Analysis of known-age data revealed that annual survival of *M. velifer* was strongly age-specific, with lowest survival for juveniles and survival generally increasing with age (Fig. 4A). Although survival rates were similar between juvenile males and females, females generally survived better than males for older age classes. Juveniles frequently have lower survival than older individuals in most vertebrates, including bats (Oli and Dobson 2003; O'Shea et al. 2004; Stahl and Oli 2006; Kneip et al. 2011), but lack of sex-specific differences are common. Thus, *M. velifer* in this study resembled the mammalian norm of lower survival of males among adults but differed from the norm in having similar survival of the sexes among juveniles. O'Shea et al. (2004) suggested that reduced survival of juvenile male bats could be attributed to greater dispersal of young males; perhaps this behavior is reduced in nonmigratory *M. velifer*.

Analysis of *M. velifer* unknown-age data (bats > 6 months old) also showed that females survived better than males (Fig. 4B). Survival of unknown-age bats increased from 1967–1968 until about 1972–1973 and then steadily declined. We infer that these changes in survival over time are related to the increasing age of the bats and to events occurring in specific years, rather than a temporal trend, because marking of new animals ceased in 1968. Sharp decline in survival after 1973 may indicate survival senescence, although inferences for the latter years are uncertain because a very low number of bats remained alive then. Higher survival of females than males among winter-banded bats has been commonly observed in descriptive studies of bat population dynamics (e.g., Humphrey and Cope 1976, 1977). However, the opposite has also been observed (e.g., Sluiter et al. 1956), and the differences often are not large. We suggest that these simply reflect the balance of high- and low-risk behaviors by which the sexes satisfy their biological needs in their locales. If any general pattern is to be expected, it may be that populations or species needing to migrate may experience higher mortality than those not migrating, and mortality costs due to dispersal may fall disproportionately on males.

Analysis of both known-age and unknown-age data sets revealed that capture probabilities were particularly low for bats marked at Simmons Cave compared with those marked at Canyon and Vickery Caves. We consider the low probability of recapture of Simmons Cave bats to be anomalous because of 2 distinctive features of that site. Simmons Cave was not used as a hibernaculum, so all bats marked there wintered elsewhere, and their recapture rates depended on our success in surveying the locations where they overwintered. It also was the northwestern most of the core area maternity sites, so some bats marked there may have wintered in unidentified sites farther northwest, possibly quite nearby but outside the core study area. The apparently missing summer-to-winter observations on this edge of the core study area, presumably adjacent to extensive, suitable roosting sites, represents an unexpected deficiency of our sampling design caused by insufficient monitoring capability.

A potentially serious omission from the estimates of apparent survival is the absence of data for the period from birth to weaning, which causes overestimation of life expectancy. Precedents in the bat literature are few but range from 1.3% mortality in *Tadarida brasiliensis* (Herreid 1967) to 25.7% in *Lasiurus borealis* (Kunz 1971), with mortality rate inversely correlated with typical litter size (reviewed by Foster et al. 1978). We suspect that the comparable mortality rate for *M. velifer* is near the low end of this range because its maternity roosts appear to have few hazards and the species bears single young at a relatively advanced state of development. Since completion of the field work, some new mortality threats have emerged. A strip mine has begun within 1–1.5 km of 5 core area caves. If enlarged, the mine could consume occupied bat roosts. Roads to hundreds of new oil and natural gas wells have improved human access to caves, which might increase the rate of bat population visits by people. Well pressures might increase cave rockfalls due to seismic disturbances. Numerous wind-power turbines, which cause mortality of flying bats, have been built about 10 km southwest of Selman Cave, at the OU Spirit site (U.S. Geological Survey 2015). Finally, the fungus (*Geomyces destructans*) associated with white-nose syndrome in bats was reported from a *M. velifer* at Selman Cave in 2010, based on a polymerase chain reaction test followed by genetic sequencing. This finding may not be significant, however, because the pattern of infection was not consistent with white-nose syndrome observed on bats from the eastern United States, no characteristic conidia were observed, and no bat mortality was observed. Furthermore, disease surveillance conducted in the same area during winter 2010–2011 yielded negative results from the specimens collected (National Wildlife Health Center 2011).

Despite a long history of bat population research, rigorous estimates of demographic parameters using the preferred maximum-likelihood-based Cormack–Jolly–Seber model are available only for a few bat species (e.g., Keen and Hitchcock 1980; Hitchcock et al. 1984; Hoyle et al. 2001; Sendor and Simon 2003; Papadatou et al. 2009; Schorcht et al. 2009; O'Shea 2010, 2011). Application of this statistically robust method accounts for imperfect detectability in estimating survival rates, and it enables relatively reliable inferences about factors influencing survival, to the extent that such factors can be incorporated into the sampling. This study is the first to apply robust capture–mark–recapture methods to estimate survival of nonmigratory *M. velifer* and to discern sex- and age-specific patterns of survival of this little-known species.

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Supporting Information

The Supporting Information documents are linked to this manuscript and are available at Journal of Mammalogy online (jmammal.oxfordjournals.org). The materials consist of data provided by the author that are published to benefit the reader. The posted materials are not copyedited. The contents of all supporting data are the sole responsibility of the authors. Questions or messages regarding errors should be addressed to the author.

Supporting Information S1.—Population size over time, adjustment for missing values, and sample data for hibernating *M. velifer* in the core study area, plus 2 outlying caves.

Supporting Information S2.—Analysis of *M. velifer* capture probability (*P*) in Oklahoma, United States. Table S2A. Model comparison table for capture probability (*P*) for known-aged bats that were marked as juveniles in summer of 1968, using age-structured Cormack–Jolly–Seber model. Apparent survival (ϕ) in both analyses was allowed to vary over time (i.e., ϕ(time)). See Table 1 for the definition of symbols. Table S2B. Comparison for bats ≥ 6 months of age. Because actual age of these bats was unknown, age structure was not considered in this analysis.

Supporting Information S3.—Calculation of number of young born in summer maternity populations of *M. velifer* in the core study area, based on population size (flight counts) and sample data. Samples include all bats captured (those newly captured and recaptures of previously marked individuals). NA = not applicable.

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