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Recruitment in a Colorado population of big brown bats: breeding probabilities, litter size, and first-year survival

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We used mark–recapture estimation techniques and radiography to test hypotheses about 3 important aspects of recruitment in big brown bats (*Eptesicus fuscus*) in Fort Collins, Colorado: adult breeding probabilities, litter size, and 1st-year survival of young. We marked 2,968 females with passive integrated transponder (PIT) tags at multiple sites during 2001–2005 and based our assessments on direct recaptures (breeding probabilities) and passive detection with automated PIT tag readers (1st-year survival). We interpreted our data in relation to hypotheses regarding demographic influences of bat age, roost, and effects of years with unusual environmental conditions: extreme drought (2002) and arrival of a West Nile virus epizootic (2003). Conditional breeding probabilities at 6 roosts sampled in 2002–2005 were estimated as 0.64 (95% confidence interval [95% *CI*] = 0.53–0.73) in 1-year-old females, but were consistently high (95% *CI* = 0.94–0.96) and did not vary by roost, year, or prior year breeding status in older adults. Mean litter size was 1.11 (95% *CI* = 1.05–1.17), based on examination of 112 pregnant females by radiography. Litter size was not higher in older or larger females and was similar to results of other studies in western North America despite wide variation in latitude. First-year survival was estimated as 0.67 (95% *CI* = 0.61–0.73) for weaned females at 5 maternity roosts over 5 consecutive years, was lower than adult survival (0.79; 95% *CI* = 0.77–0.81), and varied by roost. Based on model selection criteria, strong evidence exists for complex roost and year effects on 1st-year survival. First-year survival was lowest in bats born during the drought year. Juvenile females that did not return to roosts as 1-year-olds had lower body condition indices in late summer of their natal year than those known to survive. DOI: 10.1644/08-MAMM-A-295.1.

Key words: big brown bats, breeding probabilities, Colorado, *Eptesicus fuscus*, fecundity, litter size, maternity colonies, recruitment, reproduction, survival

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Recruitment is a major component of population dynamics. Data necessary for understanding recruitment are rates of reproduction of females (breeding probability), number of young produced in a litter, and survival of young to reproductive age. Knowledge about sources of variation in these parameters in bat populations is limited, particularly for 1st-year survival (Frick et al. 2007; Pryde et al. 2005; Sendor and Simon 2003) and breeding probabilities. The objectives of our study were to test hypotheses about these aspects of recruitment in a population of big brown bats (*Eptesicus fuscus*) in Colorado through the study of marked individuals. In particular, we sought to test hypotheses that breeding probabilities in our study population vary by age of female, roost, prior year breeding status, and year. Estimation of conditional breeding probabilities (Nichols et al. 1994; White et al. 2006) is being applied increasingly in studies of mammals because it is an important demographic parameter that quantifies a critical component of recruitment and helps inform life-history theory (Beauplet et al. 2006; Hadley et al. 2006; Kendall et al. 2004). Our hypotheses about possible effects of the above factors on breeding probability are based on evidence from other species of bats that not all females produce young in their 1st year of life, with a delay in reaching sexual maturity thought to increase lifetime reproductive

TABLE 1.—Environmental conditions that differed among years and predicted effects on 1st-year survival or breeding probabilities of female big brown bats (*Eptesicus fuscus*) in Fort Collins, Colorado. Precipitation and Palmer Drought Severity Index (PDSI) data are for April–August each year. Lower PDSIs indicate greater drought, and a value of 99 indicates average conditions (Colorado Climate Center 2006). Sources for West Nile virus epizootic and permethrin application data are given in the text. S = estimated survival, Ψ = estimated breeding probability, NA = not applicable to estimates.

Initial year	Environmental conditions	Total precipitation (cm)	Monthly PDSI (range)	Predicted subsequent effects
2001	No extremes	21.3	−1.3 to 99	No effect on 1st-year S (Ψ not estimated).
2002	Extreme drought	9.5	−4.6 to −2.2	Year effect expected in 1st-year S. Year effect expected in Ψ in females ≥ 2 years old if drought effects on breeding are immediate
2003	No drought; West Nile virus epizootic, permethrin use	26.2	−1.5 to 1.6	Year effect expected in 1st-year S if susceptible to mortality from West Nile virus or permethrin. Year effect expected in Ψ in females ≥ 2 years old if drought effects from 2002 delayed, or if breeding impacted by virus (permethrin applied after breeding)
2004	No drought	29.7	−3.1 to 2.9	NA
2005	No drought	26.6	2.4 to 5.1	NA

success (Racey and Entwistle 2000; Tuttle and Stevenson 1982). A limited amount of evidence also exists for year effects on recruitment in bats due to annual differences in weather patterns (Grindal et al. 1992; Lewis 1993; Ransome and McOwat 1994), including curtailed breeding during years with prolonged drought (Rhodes 2007). Reproductive success in big brown bats has been suggested to vary by roost (Lausen and Barclay 2006) due to differences among roosts in favorability of thermal environments; to our knowledge the effects of prior year reproduction on breeding probability have not been examined in bats. We also tested the hypothesis that the occurrence of singletons or twins corresponds with age or size of mothers.

First-year survival was the 3rd key component of recruitment that we evaluated for hypothesized effects of age, roost, year of study, and their possible interactions. We predicted that 1st-year survival would be lower than survival of older bats. This can occur if young of the year have greater vulnerability to predators than adults or an inability to gain sufficient energy stores for successful hibernation. Evidence exists for differential 1st-year survival in other species of bats (reviewed in O'Shea et al. 2004). Year effects were an important aspect of hypothesis testing for both breeding probabilities and survival because the study area suffered a severe drought during 1 year (Pielke et al. 2005), and another year was marked by the arrival of the most virulent phase of the North American epizootic of West Nile virus (Bode et al. 2006; Nemeth et al. 2007), with accompanying application of insecticide for vector control (Bolling et al. 2007). Year effects in breeding probabilities and survival were predicted if this population was impacted negatively by the different environmental conditions that occurred in these 2 years. Research on possible impacts of West Nile virus infection on big brown bat populations has been encouraged (Bunde et al. 2006; Pilipski et al. 2004), and effects of modern insecticides on bat reproduction and survival are poorly known (O'Shea and Johnston 2009).

Few modern ecological studies of bats have been conducted with the objectives of testing hypotheses about sources of variation in vital parameters (e.g., Frick et al. 2007; Pryde et al. 2005; Sendor and Simon 2003). This stands in contrast to a large number of studies in the 1960s and 1970s that used banding and ad hoc analytical methods to investigate bat population dynamics (for reviews see O'Shea et al. 2004; Racey 1982; Tuttle and Stevenson 1982), later curtailed due to concerns about banding injuries (e.g., Baker et al. 2001; Jones 1976) and disturbance within nursery roosts (Sheffield et al. 1992). In this study we intentionally used more contemporary mark–recapture analytical techniques (e.g., Lebreton et al. 1992; White et al. 2006), alternative marking and detection methods, and noninvasive evaluation of litter size.

MATERIALS AND METHODS

Study area, study population, and environmental conditions.—We studied big brown bats in Fort Collins, Colorado, elevation 1,525 m. Climate is temperate and semiarid, with average annual precipitation of 36.8 cm and average monthly temperatures of −2°C in January and 22°C in July (Colorado Climate Center 2006). Big brown bats roost in buildings in the city during the summer, migrating to higher elevations in the mountains to hibernate in rock crevices in autumn (Neubaum et al. 2006, 2007). We located maternity colonies by radiotracking bats captured over water in parks and city-designated natural areas, and through local knowledge. The population is dominated by adult females and young; adult males are more common at higher elevations in the adjacent Rocky Mountains (Neubaum et al. 2006). Roosts where we sampled were chosen based on logistic and access considerations.

Each of the first 3 years of the study (2001–2003) had differences in potentially important environmental events. The area experienced severe drought in 2002 (Table 1). Drought can reduce the abundance of insects in temperate zones (e.g., Frampton et al. 2000) and thus impact reproduction in insectivorous bats (Rhodes 2007). We documented the comparative extent of the drought for each year of the study by compiling total precipitation and the monthly Palmer Drought Severity Index (Table 1) for the warm-season period

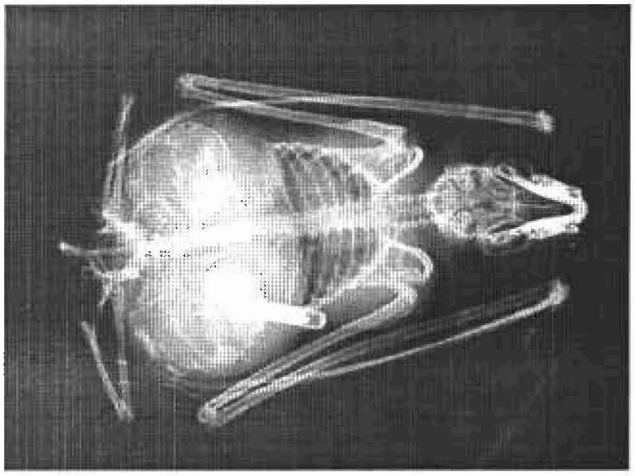

FIG. 1.—Radiograph of a near-term pregnant female big brown bat (*Eptesicus fuscus*) with twin fetuses. Also note the presence of the passive integrated transponder (PIT) tag, which has migrated subdermally away from its original dorsal insertion point.

when bats are most active (April–August) based on the data available for Fort Collins and Colorado Zone 11, north Front Range, and adjacent plains (Colorado Climate Center 2006). The index is a standardized method for measuring intensity, duration, and spatial extent of drought based on precipitation, air temperature, and local soil moisture, with values ranging from −6.0 (extreme drought) to +6.0 (Heim 2002; National Climatic Data Center 2007). In addition to drought, the area experienced the arrival of the most virulent phase of the North American epizootic of West Nile virus in 2003 (Bode et al. 2006; Nemeth et al. 2007). As a result, the pyrethroid permethrin (a general insecticide) was applied for public health purposes in August 2003 to control mosquito vectors (Bolling et al. 2007).

Capture, handling, marking, and assessment of reproductive status.—We captured bats as they emerged from maternity roosts at dusk (bats were captured internally only at 1 roost) using mist nets, harp traps, funnel traps, and handheld nets. Bats were transported to the laboratory where they were tagged, sampled, and examined under full illumination (described in detail by Wimsatt et al. [2005]); bats were released at the roost on the night of capture. We individually tagged bats (n = 2,968 females) by subdermal insertion of passive integrated transponder (PIT) tags (AVID, Inc., Norco, California) at the lower dorsum on their 1st capture (Wimsatt et al. 2005), and all bats were scanned by handheld PIT tag readers at least twice during each subsequent capture. Age (volant juvenile or adult) and reproductive condition were assessed based on criteria in Anthony (1988) and Racey (1988).

We attempted to assess litter size in females in late gestation by palpation and evaluated the accuracy of this technique by subsequent euthanization (with a ketamine–xylazine overdose) and dissection (n = 41). Palpation was unreliable for assessing litter size, and in 2005 we instead determined litter sizes in a larger sample of near-term pregnant female bats using radiography (Fig. 1). These bats were captured on 5 nights between 6 and 13 June and transported to the radiology facility at the Colorado State University Veterinary Teaching Hospital. Cloth bags with bats were taped to radiographic cassettes (5 bags per cassette) and exposed under a Mammoview low-dose mammography instrument (General Electric, Milwaukee, Wisconsin), then released at the roost the same night. To avoid undue disturbance at maternity colonies, we did not regularly capture bats within roosts and have no data on young prior to fledging. We assume that preweaning mortality is low (1–7% in North American vespertilionids that do not give birth over water—Christian 1956; Holroyd 1993; Humphrey et al. 1977; O'Farrell and Studier 1973). Capture, marking, sampling, and euthanization followed guidelines of the American Society of Mammalogists (Gannon et al. 2007) and were approved by the Institutional Animal Care and Use Committees of Colorado State University and the United States Geological Survey. Bats were captured under authority of a scientific collecting license issued by the Colorado Division of Wildlife.

Estimation of conditional breeding probabilities, 1st-year survival, and body condition.—We used 2 different data sets to calculate breeding probabilities (see statistical methods later in text) and a 3rd data set for estimation of 1st-year survival. These different data sets were used to take advantage of the largest possible sample sizes for testing different hypotheses. We based the initial analysis of breeding probabilities on known-age individual adult females physically captured and examined for evidence of breeding at the 6 roosts sampled each year in June and July. The 2nd analysis was based on a larger data set consisting of all adults captured and examined at these 6 sites categorized as 2 years old or older (adults of unknown age entered into computations only the year after 1st capture as an adult). These data were used to assess year and roost effects on estimated breeding probabilities of females older than yearlings, based on reproductive status records in 2002–2005 (see "*Data analysis*"). Reproductive status (or state) was categorized as nonbreeding or breeding (pregnant, lactating, or postlactating). Our estimates of breeding probabilities assume that the rate of misclassification of breeding status during this period is low. We had 372 cases where we recaptured individual adult females in hand more than once during June–July within a year (up to 4 recaptures). Diagnoses of breeding status (e.g., nonreproductive versus pregnant, lactating, or postlactating) were conflicting in just 15 cases (4%), supporting the assumption of a low rate of misclassification. Our methods also assume that bias from nonreproductive bats failing to use maternity roosts is small. One study found this assumption to be the case for most bats (Barclay et al. 2004) but reported exceptions and suggested caution. We have limited data that indicate this bias was small in our study. We captured 79 adult female big brown bats over water (considered random by criteria of Barclay et al. [2004]) away from roosts between 10 June and 20 July 2001–2005: 72 (91.1%) were breeding (95% confidence interval [95% *CI*] =

85–97%). We captured 2,521 adult females emerging from maternity roosts over the same period and 2,333 (92.5%) were reproductive (95% *CI* = 91–94%).

We used a sampling technique for estimation of 1st-year survival that was different than that used for estimating breeding probability. This allowed larger sample sizes because it did not require physically examining bats. Previous methodological research comparing the 2 methods of sampling (capture versus passive encounters by PIT tag readers) show that higher capture probabilities and more precise survival estimates are obtained using passive detection (Ellison et al. 2007). We deployed hoop-style PIT tag readers over the openings of roosts to monitor the entrance and exit dates and times of tagged bats automatically (Ellison et al. 2007; O'Shea et al. 2004; Wimsatt et al. 2005). This allowed us to examine records for evidence of returns of bats each year as "captures" (encounters) for estimation of juvenile 1st-year survival (see "*Data analysis*"). Although bats at some roosts could use additional openings that lacked PIT tag readers, only 1 detection per year was necessary for annual survival estimation, and the high encounter probabilities derived from this technique demonstrate its assumed efficiency (Ellison et al. 2007). We assigned a body condition index to juvenile female bats captured in late summer (2–3 September 2003, 30–31 August 2004, and 7 September 2004) at roosts monitored with PIT tag readers. This index was the ratio of body mass to length of forearm (Speakman and Racey 1986) validated for this population by total lipid analysis (Pearce et al. 2008). We compared indices in bats that did not return to the 95% *CI*s of mean condition indices of bats that returned. These comparisons were limited to bats initially captured at the same roost on the same dates because of expected differences in condition with date (Pearce et al. 2008).

Data analysis.—We used an information-theoretic approach for data analysis (Burnham and Anderson 2002). We computed breeding probabilities and 1st-year survival estimates using program MARK (White and Burnham 1999; White et al. 2006). We used multistate capture–recapture models to estimate known-age bat breeding probabilities (at 1–4 years of age) and probability of breeding for females 2 years old or older. The multistate model of Brownie et al. (1993) and Hestbeck et al. (1991) is an extension of the Cormack–Jolly–Seber live recapture model. In addition to survival and capture or encounter probabilities, this model enables consideration of transition probabilities among strata or states (age and reproductive status—White et al. 2006). A change in reproductive status or state (nonbreeder to breeder, or vice versa) between years constitutes a bat transitioning or changing states and allows for the estimation of a breeding probability. Our 1st analysis estimated breeding probabilities of known-age bats (bats marked as juveniles and recaptured in later years). The 2nd analysis was based on a larger sample that included females of unknown ages at least 2 years or older (based on 1st capture the previous year when 460 adult bats were marked and recaptured as adults). We tested for year and roost effects on breeding probabilities in this 2nd analysis.

For the multistate analysis of known-age bats, we assigned individuals to 9 states based on age and reproductive status (juvenile, 1-year breeder, 1-year nonbreeder, 2-year breeder, 2-year nonbreeder, 3-year breeder, 3-year nonbreeder, 4-year breeder, and 4-year nonbreeder). Some transitions are not possible (i.e., 2-year breeder to 1-year breeder or nonbreeder); we set these transitions to 0 in MARK. We examined 5 models to assess the effects of state (reproductive status and age) on survival, capture, and breeding probabilities (models listed in Appendix I). We could not include roost as a covariate in this analysis of known-age bats because of sample-size limitations. For the analysis of breeding probabilities of adults 2 years old or older, we assigned bats to 1 of 2 states (breeder or nonbreeder). Models considered for this analysis included the following main effects and their interactions on survival, capture, and breeding probabilities: reproductive status (state); year-to-year variation (year); effects of 6 different roosts (roost); and interactions of state, roost, and year. We also included models with survival, capture, and breeding probability as constant (.). This resulted in a set of 14 candidate models (Appendix I). We did not include models with an age structure in the 2nd analysis because precise age was unknown (all bats were more than 2 years old).

We estimated 1st-year postweaning and adult survival from 2001 to 2005 using an age-based Cormack–Jolly–Seber model (White and Burnham 1999) with encounter histories from a larger data set (n = 557 juvenile females) than that used for estimating 1st-year breeding probabilities. Unlike the breeding probability studies, this data set did not require physical capture of bats after marking but instead was based on encounters obtained through automatic registration of PIT tag numbers by hoop readers. Estimates were for "apparent survival" because they cannot distinguish between death and permanent emigration (White and Burnham 1999). We constructed a set of 13 a priori candidate models (Appendix I). These models included the following main effects and their interactions on survival (ϕ) and encounter probabilities (p): age structure (age); effects of 5 different roosts (roost); year-to-year variation (year); and interactions of age, roost, and year. We also included a model with apparent survival and encounter probabilities as constant (.) across age, roost, and year. We also were interested in the additive effects of year on survival so we included a model in our candidate set that examined survival varying by age and roost with the parallel effects of year (age × roost + year). For models including age structure, 1st-year postweaning juveniles were considered adults the year following birth and were modeled as adults in succeeding years. We constructed an input file for program MARK with 5 encounters (years) and 2 age classes (or groups): juveniles and adults. All individuals born and initially marked in a given summer belong to the same birth cohort. We created an age-based structure in program MARK as the basis for further model building and selection (Cooch and White 2006). We also calculated an overall population-wide estimate for juvenile and adult survival by constraining survival to be constant across roosts and time, and estimated

1st-year survival at 1 additional roost with 4 consecutive years of encounter data (2002–2005) to better assess variation in juvenile survival estimates.

The fit of competing models in our breeding probability and survival analyses were assessed using information-theoretic methods (Burnham and Anderson 2002). Models were ranked using Akaike's information criterion corrected for sample size (AIC_C—Burnham and Anderson 2002). We also calculated AIC_C differences (Δ_i; difference in AIC_C score between ith and top-ranked model), Akaike weights (w_is; probability that the ith model is the best approximating model among candidate models), and evidence ratios (the ratio of model weights for the top model and the next highest ranking model). The variance inflation factor ($\hat{c}$) was used as an estimate of goodness-of-fit of the models with $\hat{c}$ values of 1.0 indicating good fit, and values of 1–3 acceptable fit of the data to the models (Lebreton et al. 1992). We assessed the goodness-of-fit of models using the median-$\hat{c}$ approach and estimated $\hat{c}$ using a lower bound of 1.0, an upper bound of 5.0, 10 intermediate points, and 10 replicates at each point (Cooch and White 2006). AIC_C values were converted to Akaike's information criterion corrected for overdispersed data and small sample sizes ($QAIC_C$) values to adjust for overdispersion. We selected the most-parsimonious models using a combination of $QAIC_C$, $\Delta QAIC_C$, and $QAIC_C$ weights (w—Burnham and Anderson 2002; Lebreton et al. 1992). Models with $\Delta QAIC_C \geq 2$ were not considered competitive with the highest ranked model (Burnham and Anderson 2002).

Results

Annual breeding probabilities.—Annual breeding probability estimates (conditional on survival and capture probabilities) of known-age adult female bats 1st captured as juveniles at 6 maternity roosts ranged from 0.64 at 1 year of age to 0.90 or more in older bats (Table 2). These estimates were based on 392 bats 1st captured and tagged as juveniles at 6 maternity roosts between 2001 and 2004 and examined for breeding status when recaptured at 1 year old (n = 83 bats), 2 years old (n = 59), 3 years old (n = 30), and 4 years old (n = 15). Breeding probabilities were lowest in 1-year-old females, and 95% *CI*s were nonoverlapping with those for breeding probabilities of older bats (Table 2). Once females reached age 2 years, the probability of breeding increased to 0.90 or higher, with broadly overlapping 95% *CI*s between estimates for 2-year-old females that had or had not bred as 1-year-olds (Table 2). Conditional breeding probabilities were very high for 3- and 4-year-olds with overlapping 95% *CI*s (Table 2). The highest ranking model had breeding probabilities differing by state (age and reproductive status) and constant survival and capture probabilities (Appendix I). This model had an evidence ratio of 12.6:1 over the next highest ranking model.

Breeding probabilities of females 2 or more years old were very high (Table 3). This data set included 460 individuals captured at 6 roosts (number of marked bats at each roost $\bar{X}$ = 77 ± 24 *SE*, range 23–187). The top-ranked model incorporated survival probability as constant, capture probability as a function of roost, and breeding probability as a function of breeding state (Appendix I). This model had an evidence ratio of 15:1 over the next highest ranking model; models including roost and year effects on survival and breeding probabilities had negligible support based on AIC_C weights.

Table 2.—Conditional annual breeding probabilities (Ψ, transition probability of breeding at the subsequent age) of individually marked, known-age big brown bats (*Eptesicus fuscus*) captured and examined in hand at 6 maternity roosts in Fort Collins, Colorado, 2002–2005. Probabilities of a bat moving to nonbreeding status are approximately (1.00 − Ψ) for each age group. Dashes occur where probabilities were inestimable (in both cases only 1 bat did not breed at ages 3 or 4 years). Effects of calendar year or roost were not examined in this data set because of sample size limitations.

Age (years) and prior year status	Subsequent age (years)	Ψ	95% *CI*
Juvenile	1	0.64	0.53–0.73
Age 1 breeder	2	0.90	0.78–0.97
Age 1 nonbreeder	2	0.94	0.76–1.00
Age 2 breeder	3	0.96	0.84–1.00
Age 2 nonbreeder	3	—	—
Age 3 breeder	4	0.97	0.75–1.00
Age 3 nonbreeder	4	—	—

Litter size.—Litter size in near-term pregnant bats sampled at 5 roosts in 2005 included 100 females with singletons and 12 (10.7%) with twins, for a mean litter size of 1.11 (95% *CI* = 1.05–1.17). In a subsample of known-age and known–minimum-age bats we found no relationship between increased age and litter size: twins were carried by 8 (12.3%) of 65 bats 4 or more years old (litter size $\bar{X}$ = 1.12, 95% *CI* = 1.04–1.21); more precise ages were available only for 14 of the radiographed bats). Twins occurred at 3 of the 5 roosts, but our sample sizes at some roosts were small, precluding statistical comparison by roost. Mean length of forearm was nearly identical in females with litter sizes of 1 ($\bar{X}$ = 47.2 mm, 95% *CI* = 46.9–47.5 mm; n = 98) and 2 ($\bar{X}$ = 47.1 mm, 95% *CI* = 45.6–48.6 mm; n = 9), providing no evidence for higher twinning rates in larger females.

First-year survival of juvenile females.—The overall survival rate for juvenile females for the 1st year of life, based on encounters with PIT tag readers during 2001–2005, was 0.67 (95% *CI* = 0.61–0.73; Table 4) compared to the adult rate of 0.79 (95% *CI* = 0.77–0.81; calculated using model ϕ(age) p(age)). Juvenile survival at the additional roost with 4 years of encounter histories was similar to the 5-year estimate for the other 5 roosts: 0.63 (95% *CI* = 0.47–0.78), as was the adult rate of 0.78 (95% *CI* = 0.72–0.84). First-year survival varied among the 3 years (across all roosts) and was lowest for bats born in the drought year of 2002 but highest in the year of the West Nile virus epizootic (Table 4). First-year survival based on roost was variable, but with overlapping confidence intervals. When estimated by both year and roost, 1st-year survival of juvenile females ranged from 0.08 to 0.88. The

TABLE 3.—Conditional annual breeding probabilities (Ψ, transition probability of breeding at the subsequent age) for adult female big brown bats (*Eptesicus fuscus*) 2 years old or older (n = 460) captured and examined at 6 maternity roosts in Fort Collins, Colorado, 2002–2005. Estimates are based on the highest ranking model out of a set of 14 candidate models (Appendix I).

Prior year status	Subsequent year status	Ψ	95% *CI*
Breeder	Breeder	0.96	0.94–0.98
Breeder	Nonbreeder	0.04	0.02–0.06
Nonbreeder	Breeder	0.94	0.61–0.99
Nonbreeder	Nonbreeder	0.06	0.01–0.38

pattern of lower estimates during 2002 held for most of the roosts, but with wide confidence intervals (Table 4).

The highest ranking model for 1st-year survival was a function of variable encounter probabilities by roost, with survival probability a function of complex interactions between year, roost, and age (this model had an evidence ratio of 11.5:1 over the 2nd highest ranking model in the candidate set of models: Appendix I). Annual encounter probabilities of juvenile and adult females were high at individual roosts and provide strong evidence for natal philopatry. Encounter probability for juvenile females across all 5 roosts was 0.98 (95% *CI* = 0.93–0.99) and for adult females was 0.99 (95% *CI* = 0.97–0.99). Results from model selection indicated no age effect on subsequent encounters, but strong evidence that encounter probabilities varied by roost was obtained. Natal philopatry also was inferred from the tagging of 557 juvenile female bats at multiple roosts in the first 4 years of the study. Just 12 were encountered at roosts other than their natal colony sites in subsequent years (of 357 females detected after their year of birth). Only 1 of these 12 individuals switched to a different monitored colony. Seven of the remaining 11 bats used alternate colonies for a single night and 4 did so for 3–13 nights.

Body condition of 69 juvenile females measured in late August and September was compared between bats that returned in subsequent years and those that failed to return. We captured 29 juvenile females on 2–3 September 2003. Twenty-seven of these returned in 2004 or 2005. Body condition indices of the 2 that did not return (0.37 and 0.38) were less than the mean and less than or equal to the lower confidence limit (*CL*) for indices of the 27 females that returned ($\bar{X}$ = 0.40, 95% *CI* = 0.38–0.42). Sixteen juvenile female bats were sampled on 30–31 August 2004. Three of these failed to return the subsequent year and had body condition indices (0.28, 0.31, and 0.33) less than or equal to the lower *CL* for the 13 juvenile females in the group known to survive ($\bar{X}$ = 0.36, 95% *CI* = 0.33–0.39). On 7 September 2004 we determined condition indices for 27 juvenile females. The upper *CL* for the mean body condition index of 16 juvenile females ($\bar{X}$ = 0.40; 95% *CI* = 0.38–0.43) that did not return in 2005 was equal to the lower *CL* for the 11 bats captured that night and known to be alive the next summer ($\bar{X}$ = 0.46; 95% *CI* = 0.43–0.48).

DISCUSSION

Breeding probabilities of 1-year-old female big brown bats were lower than in older known-age bats. Once bats reached ages 2–4 years the probability of breeding was consistently high, ranging from 0.90 to 0.97. Bats that were 2 years old or older had very high probabilities of breeding each year, with only a 0.04–0.06 chance of not breeding in a subsequent year. Lower fecundity in 1-year-old bats is consistent with findings based on simple reproductive rate calculations (percent pregnant or lactating) from studies of big brown bats in other areas of North America (Brigham and Fenton 1986; Schowalter and Gunson 1979; Sidner 1997). Once female big brown bats reached age 2 years in the Colorado population, the probability of breeding each year was very high and conditional on a constant survival probability and capture probabilities varying by roost. Breeding probabilities did not vary by year or roost. An assumed constant rate commonly is observed in models of adult survival in long-lived mammals (e.g., Gaillard et al. 2000), and variable capture probabilities by roost were expected because each building presented different logistical situations for capture of bats in nets or other devices. Lack of a year effect on adult

TABLE 4.—Estimates of 1st-year postweaning survival ($\hat{\phi}$) of juvenile female big brown bats (*Eptesicus fuscus*) at 5 maternity roosts monitored from 2001 to 2005 in Fort Collins, Colorado. Estimates and 95% confidence intervals (95% *CI*s) are provided for bats at each roost for each of 3 annual periods based on passive encounters registered by passive integrated transponder (PIT) tag readers. Estimates for bats at each roost within a year are from the best approximating model: ϕ(age + roost × year) p(roost) (see Appendix I), and the estimate for bats over all years and roosts combined is in the lower right cell of the table (based on the model ϕ(age) p(age)). Estimates of 1st-year survival of bats also are provided for each year across all roosts (estimates from model ϕ(age + roost) p(roost)) and for each roost across all years (estimates from model ϕ(age × year) p(roost))

Roost	Born in 2001 $\hat{\phi}$ (95% *CI*)	Born in 2002 $\hat{\phi}$ (95% *CI*)	Born in 2003 $\hat{\phi}$ (95% *CI*)	Each roost across all years $\hat{\phi}$ (95% *CI*)
HFA	0.72 (0.56–0.84)	0.68 (0.50–0.82)	0.84 (0.65–0.94)	0.71 (0.62–0.79)
PET	0.62 (0.31–0.86)	0.33 (0.07–0.78)	0.72 (0.40–0.91)	0.77 (0.62–0.87)
CR4	0.88 (0.55–0.98)	0.08 (0.01–0.50)	0.45 (0.15–0.79)	0.51 (0.35–0.67)
LAH	Inestimable	0.50 (0.04–0.96)	0.67 (0.11–0.97)	0.75 (0.32–0.95)
TAH	0.48 (0.29–0.68)	0.57 (0.19–0.88)	0.78 (0.49–0.93)	0.59 (0.44–0.73)
Each year across all roosts	0.67 (0.57–0.77)	0.52 (0.38–0.65)	0.76 (0.63–0.85)	Overall 0.67 (0.61–0.73)

breeding probability is particularly instructive in the context of the drought in 2002 and the arrival of the West Nile virus epizootic and application of permethrin in 2003. The lack of a year effect in 2003 is consistent with findings that big brown bats are insensitive to West Nile virus when dosed by experimental inoculation in captive experiments (Davis et al. 2005). The lack of a roost effect on breeding probabilities also suggests that all of the sites we sampled may provide required thermal conditions for pregnancy and lactation in adult females. Lower breeding probabilities of 1-year-olds is evidence that some bats of this age class might lack sufficient nutritional reserves in spring and early summer to allow successful parturition and lactation. These bats defer reproduction until age 2 years or older. We speculate that the lack of a year effect and the high breeding probabilities observed in bats 2 or more years old also may indicate that the urbanizing environment supporting our study population is favorable to big brown bat demography. This species is typically the most abundant bat in urban and suburban areas of North America (e.g., Johnson et al. 2008; Kurta and Teramino 1992; Loeb et al. 2009).

Big brown bats are geographically bimodal in litter size, with litters of 2 in eastern and 1 in western North America. It is unknown why litter size in this species is partitioned so strongly by longitude but not latitude. Data for litter sizes of big brown bats in western North America span 2,500 km in latitude and a diversity of habitat and climatic conditions, with representative studies in Arizona, Colorado, and Alberta, Canada. In the southern Arizona desert, 3 colonies of banded big brown bats roosting in bridges were sampled intensively for 12–14 years; similar to our study, litter size was 1.1–1.2 (Sidner 1997). Litter size was 1.13 (nearly identical to Colorado) in Alberta (Holroyd 1993; Schowalter and Gunson 1979). A sharper longitudinal than latitudinal gradient in litter size of big brown bats exists: 590 km east of our study area litter size was 2.0 in Kansas (Kunz 1974), and modal litter size is also 2 throughout central and eastern North America (Christian 1956; Cockrum 1955; Kurta and Baker 1990). The ecological or historical factors that have resulted in this remarkable longitudinal dichotomy in litter size are unknown, a point that illustrates how little is understood concerning forces that mold aspects of life history in even the most common bats.

Three other studies applied Cormack–Jolly–Seber models to estimate 1st-year survival in microchiropterans. First-year survival was lower than adult survival in pipistrelles (*Pipistrellus pipistrellus*) in Germany (Sendor and Simon 2003) and in long-tailed bats (*Chalinolobus tuberculatus*) in New Zealand (Pryde et al. 2005). Years with different weather and predator conditions influenced survival in long-tailed bats. Juvenile survival in Yuma myotis (*Myotis yumanensis*) banded at maternity colonies and night roosts in bridges and buildings in California also was lower than in adults (Frick et al. 2007). Most past research on survival in bats generally relied on ad hoc analyses that did not adjust for capture probability, used bands that can affect survival, and marked bats at hibernacula when juveniles could not be distinguished from adults (O'Shea et al. 2004). However, estimates of 1st-year survival in other species of temperate zone North American bats derived from such approaches have generally been lower and less precise than our overall estimate (e.g., Humphrey and Cope 1970; Pearson et al. 1952; Sidner 1997; Stevenson and Tuttle 1981). This could be due not only to our application of analytical techniques that incorporate capture probability (1st-year survival in the Yuma myotis also was high relative to these past studies—Frick et al. 2007) but also to the passive method of detection using PIT tag readers, which results in higher encounter probabilities and greater precision of estimates than those made through direct captures (Ellison et al. 2007). Estimated 1st-year survival rates in our study were higher than ad hoc (life-table) estimates for big brown bats in Arizona (Sidner 1997), which showed lower survival in juveniles than in adults and higher return rates of juveniles that were in better body condition the previous summer. In our study juveniles that were not known to be alive as adults also had lower body condition indices in late August and early September of the year of birth compared to bats known to return, consistent with studies of other temperate zone bats that concluded that entry into hibernation in good body condition is a prerequisite for survival to the ensuing year (Davis 1966; Humphrey and Cope 1977; Ransome 1990).

We found no evidence for negative effects on 1st-year survival in the cohort of big brown bats born during the year with arrival of the West Nile virus epizootic. Unlike breeding probabilities, 1st-year survival varied with roost and year through complex interactions between these 2 effects and age. The estimates of survival were generally lower in 1st-year bats born during the drought year, suggesting that this drought may have affected big brown bat demography more through juvenile survival than through adult breeding probability. Model selection results also suggest that this effect might vary by roost. The importance of the roost environment for sustaining bat populations has long been recognized (Kunz 1982). First-year survival might be more variable than adult breeding probability among the anthropogenic structures used as roosts in our study. This variability could relate to at least 2 factors: fledged juveniles could be at energetic disadvantages or have greater vulnerability to predators at some roosts. We did not test for these effects directly but noted lower body conditions indices in juveniles not known to return after their year of birth. Additionally, 2 roosts with low survival in some years were observed to be visited by domestic cats that stalked bats during emergence. These sites had emergence points closer to the ground than roosts with higher survival, and inexperienced and less agile fledglings could have been easier prey at these roosts.

Recruitment in the study population of big brown bats involved high breeding probabilities in adult females 2 years old or older, low variability in litter size, and lower survival and breeding probabilities in 1-year-olds than in adults. Breeding probability in adults did not vary by roost or year, but 1st-year survival varied with these 2 factors in complex ways. The suggested negative influence of drought on 1st-year survival has implications for the conservation of bat

populations given projections of climate change models for greater drought conditions over large areas of western North America (Barnett et al. 2008; Seager et al. 2007). This work also demonstrates that alternative marking and recapture methods coupled with modern statistical approaches can be employed profitably in the study of vital parameters crucial to recruitment in bat populations. We hope that approaches similar to those we used with this common species will be considered in future studies of other species of bats to advance understanding of their population dynamics. The deteriorating conservation status of many bat populations dictates a need for improved understanding of vital parameters to better gauge progress in achieving management goals.

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Literature Cited

Anthony, E. L. P. 1988. Age determination in bats. Pp. 47–58 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

Baker, G. B., et al. 2001. The effect of forearm bands on insectivorous bats (Microchiroptera) in Australia. Wildlife Research 28:229–237.

Barclay, R. M. R., et al. 2004. Variation in the reproductive rate of bats. Canadian Journal of Zoology 82:688–693.

Barnett, T. P., et al. 2008. Human-induced changes in the hydrology of the western United States. Science 319:1080–1083.

Beauplet, G., C. Barbaud, W. Dabin, C. Kussener, and C. Guinet. 2006. Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. Oikos 112:430–441.

Bode, A. V., J. J. Sejvar, W. J. Pape, G. L. Campbell, and A. A. Marfin. 2006. West Nile virus disease: a descriptive study of 228 patients hospitalized in a 4-county region of Colorado in 2003. Clinical Infectious Diseases 42:1234–1240.

Bolling, B. G., C. G. Moore, S. L. Anderson, C. D. Blair, and B. J. Beaty. 2007. Entomological studies along the Colorado Front Range during a period of intense West Nile virus activity. Journal of the American Mosquito Control Association 23:37–46.

Brigham, R. M., and M. B. Fenton. 1986. The influence of roost closure on the roosting and foraging behaviour of *Eptesicus fuscus* (Chiroptera: Vespertilionidae). Canadian Journal of Zoology 64:1128–1133.

Brownie, C., J. E. Hines, J. D. Nichols, K. H. Pollock, and J. B. Hestbeck. 1993. Capture–recapture studies for multiple strata including non-Markovian transitions. Biometrics 49:1173–1187.

Bunde, J. M., E. J. Heske, N. E. Mateus-Pinilla, J. E. Hofmann, and R. J. Novak. 2006. A survey for West Nile virus in bats from Illinois. Journal of Wildlife Diseases 42:455–458.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd ed. Springer-Verlag, New York.

Christian, J. J. 1956. The natural history of a summer aggregation of the big brown bat, *Eptesicus fuscus fuscus*. American Midland Naturalist 55:66–95.

Cockrum, E. L. 1955. Reproduction in North American bats. Transactions of the Kansas Academy of Science 58:487–511.

Colorado Climate Center. 2006. Data access. http://ccc.atmos.colostate.edu. Drought resources: Colorado modified Palmer index. http://ccc.atmos.colostate.edu/palmerindex.php. Accessed 25 October 2006.

Cooch, E., and G. White (eds.). 2006. Program Mark, a gentle introduction. 8th ed. http://www.phidot.org/software/mark/docs/book. Accessed 7 July 2009.

Davis, A., M. Bunning, P. Gordy, N. Panella, B. Bettvich, and R. A. Bowen. 2005. Experimental and natural infection of North American bats with West Nile virus. American Journal of Tropical Medicine and Hygiene 73:467–469.

Davis, W. H. 1966. Population dynamics of the bat *Pipistrellus subflavus*. Journal of Mammalogy 47:383–396.

Ellison, L. E., T. J. O'Shea, D. J. Neubaum, M. A. Neubaum, R. D. Pearce, and R. A. Bowen. 2007. A comparison of conventional capture versus PIT reader techniques for estimating survival and capture probabilities of big brown bats. Acta Chiropterologica 9:149–160.

Frampton, G. K., P. J. Van Den Brink, and P. J. L. Gould. 2000. Effects of spring drought and irrigation on farmland arthropods in southern Britain. Journal of Applied Ecology 37:865–883.

Frick, W. F., W. E. Rainey, and E. D. Pierson. 2007. Potential effects of environmental contamination on Yuma myotis demography and population growth. Ecological Applications 17:1213–1222.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toigo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gannon, W. L., R. S. Sikes, and the Animal Care and Use Committee of the American Society of Mammalogists. 2007. Guidelines of the American Society of Mammalogists for the use of wild mammals in research. Journal of Mammalogy 88:809–823.

Grindal, S. D., T. S. Collard, R. M. Brigham, and R. M. R. Barclay. 1992. The influence of precipitation on reproduction by Myotis bats in British Columbia. American Midland Naturalist 128:339–344.

Hadley, G. L., J. J. Rotella, R. A. Garrott, and J. D. Nichols. 2006. Variation in probability of first reproduction of Weddell seals. Journal of Animal Ecology 75:1058–1070.

Heim, R. R., Jr. 2002. A review of twentieth-century drought indices used in the United States. Bulletin of the American Meteorological Society 83:1149–1165.

Hestbeck, J. B., J. D. Nichols, and R. A. Malecki. 1991. Estimates of movement and site fidelity using mark–resight data of wintering Canada geese. Ecology 72:523–533.

HOLROYD, S. L. 1993. Influence of some extrinsic and intrinsic factors on reproduction by big brown bats (*Eptesicus fuscus*) in southeastern Alberta. M.S. thesis, University of Calgary, Calgary, Alberta, Canada.

HUMPHREY, S. R., AND J. B. COPE. 1970. Population samples of the evening bat, *Nycticeius humeralis*. Journal of Mammalogy 51:399–401.

HUMPHREY, S. R., AND J. B. COPE. 1977. Survival rates of the endangered Indiana bat, *Myotis sodalis*. Journal of Mammalogy 58:32–36.

HUMPHREY, S. R., A. R. RICHTER, AND J. B. COPE. 1977. Summer habitat and ecology of the endangered Indiana bat (*Myotis sodalis*). Journal of Mammalogy 58:334–346.

JOHNSON, J. B., J. E. GATES, AND W. M. FORD. 2008. Distribution and activity of bats at local and landscape scales within a rural–urban gradient. Urban Ecosystems 11:227–242.

JONES, C. 1976. Economics and conservation. Pp. 133–145 in Biology of bats of the New World family Phyllostomatidae. Part I (R. J. Baker, J. K. Jones, and D. C. Carter, eds.). Special Publications 10, The Museum, Texas Tech University.

KENDALL, W. L., C. A. LANGTIMM, C. A. BECK, AND M. C. RUNGE. 2004. Capture–recapture analysis for estimating manatee reproductive rates. Marine Mammal Science 20:424–437.

KUNZ, T. H. 1974. Reproduction, growth, and mortality of the vespertilionid bat, *Eptesicus fuscus*, in Kansas. Journal of Mammalogy 55:1–13.

KUNZ, T. H. 1982. Roosting ecology of bats. Pp. 1–55 in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York.

KURTA, A., AND R. H. BAKER. 1990. *Eptesicus fuscus*. American Society of Mammalogists Mammalian Species 356:1–10.

KURTA, A., AND J. A. TERAMINO. 1992. Bat community structure in an urban park. Ecography 15:257–261.

LAUSEN, C. L., AND R. M. R. BARCLAY. 2006. Benefits of living in a building: big brown bats (*Eptesicus fuscus*) in rocks versus buildings. Journal of Mammalogy 87:362–370.

LEBRETON, J. D., K. P. BURNHAM, J. CLOBERT, AND D. R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. Ecological Monographs 62:67–118.

LEWIS, S. E. 1993. Effect of climatic variation on reproduction by pallid bats. Canadian Journal of Zoology 71:1429–1433.

LOEB, S. C., C. J. POST, AND S. T. HALL. 2009. Relationship between urbanization and bat community structure in national parks of the southeastern U.S. Urban Ecosystems 12:197–214.

NATIONAL CLIMATIC DATA CENTER. 2007. Palmer drought severity index (PDSI). http://www.ncdc.noaa.gov/paleo/drought/drght_pdsi.html. Accessed 31 March 2009.

NEMETH, N. M., S. BECKETT, E. EDWARDS, K. KLENK, AND N. KOMAR. 2007. Avian mortality surveillance for West Nile virus in Colorado. American Journal of Tropical Medicine and Hygiene 76:431–437.

NEUBAUM, D. J., T. J. O'SHEA, AND K. R. WILSON. 2006. Autumn migration and selection of rock crevices as hibernacula by big brown bats in Colorado. Journal of Mammalogy 87:470–479.

NEUBAUM, D. J., K. R. WILSON, AND T. J. O'SHEA. 2007. Urban maternity roost selection by big brown bats in north-central Colorado. Journal of Wildlife Management 71:728–736.

NICHOLS, J. D., J. E. HINES, K. H. POLLOCK, R. L. HINZ, AND W. A. LINK. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture–recapture data. Ecology 75:2052–2065.

O'FARRELL, M. P., AND E. H. STUDIER. 1973. Reproduction, growth, and development in *Myotis thysanodes* and *Myotis lucifugus* (Chiroptera: Vespertilionidae). Ecology 54:18–30.

O'SHEA, T. J., L. E. ELLISON, AND T. R. STANLEY. 2004. Survival estimation in bats: historical overview, critical appraisal, and suggestions for new approaches. Pp. 297–336 in Sampling rare and elusive species: concepts, designs, and techniques for estimating population parameters (W. L. Thompson, ed.). Island Press, Washington, D.C.

O'SHEA, T. J., AND J. J. JOHNSTON. 2009. Environmental contaminants and bats: investigating exposure and effects. Pp. 500–528 in Behavioral and ecological methods for the study of bats (T. H. Kunz and S. Parsons, eds.). Johns Hopkins University Press, Baltimore, Maryland.

PEARCE, R. D., T. J. O'SHEA, AND B. A. WUNDER. 2008. Evaluation of morphological indices and total body electrical conductivity to assess body composition in big brown bats. Acta Chiropterologica 10:153–159.

PEARSON, O. P., M. R. KOFORD, AND A. K. PEARSON. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy 33:273–320.

PIELKE, R. A., ET AL. 2005. Drought 2002 in Colorado: an unprecedented drought or a routine drought? Pure and Applied Geophysics 162:1455–1479.

PILIPSKI, J. D., L. M. PILIPSKI, AND L. S. RISLEY. 2004. West Nile virus antibodies in bats from New Jersey and New York. Journal of Wildlife Diseases 40:335–337.

PRYDE, M. A., C. F. J. O'DONNELL, AND R. J. BARKER. 2005. Factors influencing survival and long-term population viability of New Zealand long-tailed bats (*Chalinolobus tuberculatus*): implications for conservation. Biological Conservation 126:175–185.

RACEY, P. A. 1982. Ecology of bat reproduction. Pp. 57–104 in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York.

RACEY, P. A. 1988. Reproductive assessment in bats. Pp. 31–45 in Ecological and behavioral methods for the study of bats (T. H. Kunz, ed.). Smithsonian Institution Press, Washington, D.C.

RACEY, P. A., AND A. C. ENTWISTLE. 2000. Life-history and reproductive strategies of bats. Pp. 363–414 in Reproductive biology of bats (E. G. Crichton and P. H. Krutzsch, eds.). Academic Press, San Diego, California.

RANSOME, R. D. 1990. The natural history of hibernating bats. Christopher Helm Publishers, Bromley, Kent, United Kingdom.

RANSOME, R. D., AND T. P. MCOWAT. 1994. Birth timing and population changes in greater horseshoe bat colonies (*Rhinolophus ferrumequinum*) are synchronized by climatic temperature. Zoological Journal of the Linnaen Society 112:337–351.

RHODES, M. 2007. Roost fidelity and fission–fusion dynamics of white-striped free-tailed bats (*Tadarida australis*). Journal of Mammalogy 88:1252–1260.

SCHOWALTER, D. B., AND J. R. GUNSON. 1979. Reproductive biology of the big brown bat (*Eptesicus fuscus*) in Alberta. Canadian Field-Naturalist 93:48–54.

SEAGER, R., ET AL. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. Science 16:1181–1184.

SENDOR, T., AND M. SIMON. 2003. Population dynamics of the pipistrelle bat: effects of sex, age, and winter weather on seasonal survival. Journal of Animal Ecology 72:308–320.

SHEFFIELD, S. R., J. H. SHAW, G. A. HEIDT, AND L. R. MCCLENACHAN. 1992. Guidelines for the protection of bat roosts. Journal of Mammalogy 73:707–710.

SIDNER, R. M. 1997. Studies of bats in southeastern Arizona with emphasis on aspects of life history of *Antrozous pallidus* and *Eptesicus fuscus*. Ph.D. dissertation, University of Arizona, Tucson.

SPEAKMAN, J. R., AND P. A. RACEY. 1986. The influence of body condition on sexual development of male brown long-eared bats (*Plecotus auritus*) in the wild. Journal of Zoology (London) 210:515–525.

STEVENSON, D. E., AND M. D. TUTTLE. 1981. Survivorship in the endangered gray bat (*Myotis grisescens*). Journal of Mammalogy 62:244–257.

TUTTLE, M. D., AND D. STEVENSON. 1982. Growth and survival of bats. Pp. 105–150 in Ecology of bats (T. H. Kunz, ed.). Plenum Press, New York.

WHITE, G. C., AND K. P. BURNHAM. 1999. Program MARK: survival estimation from populations of marked animals. Bird Study 46, supplement:120–138.

WHITE, G. C., W. L. KENDALL, AND R. J. BARKER. 2006. Multistate survival models and their extensions in program MARK. Journal of Wildlife Management 70:1521–1529.

WIMSATT, J., T. J. O'SHEA, L. E. ELLISON, R. D. PEARCE, AND V. R. PRICE. 2005. Anesthesia and blood sampling of wild big brown bats. *Eptesicus fuscus* with an assessment of impacts on survival. Journal of Wildlife Diseases 41:87–95.

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Appendix I

Model selection results for 3 analyses using program MARK. For each model we include the following terms (Burnham and Anderson 2002): number of parameters in the model (K), Akaike's information criterion adjusted for overdispersed data and small sample size ($QAIC_C$), the difference in $QAIC_C$ value between the current model and the top-ranked model ($\Delta QAIC_C$), and the Akaike weights (ws). The term $\hat{c}$ is the estimate of overdispersion. Model notation follows Lebreton et al. (1992): for analyses A and B (breeding probabilities of female big brown bats, *Eptesicus fuscus*), survival (S), capture probability (p), and transitions (Ψ were modeled as either constant across years and states (.), constant over years but different by state (state), constant over years but different by roost (roost), different by years with no roost or state differences (year), and a combination of state, roost, and year differences (state × roost × year). For analysis C (1st-year survival probabilities), apparent survival (ϕ), and capture probability (p) were modeled with an age structure (age), as constant across age and year (.), different by roost (roost), different by roost and age (roost × age), different by age and year (age × year), different among years (year), and different among roosts and age and year (age × roost × year). Analyses A and B are based on bats captured and examined in hand (required to assess breeding condition). Analysis C was conducted separately because it is based on a larger data set of passive encounters registered by automated passive integrated transponder (PIT) tag readers.

Analysis and candidate models	K	$QAIC_C$	$\Delta QAIC_C$	w
A. Breeding probabilities for known-age females ($\hat{c}$ = 3.02)				
S(.) p(.) Ψ(state)	10	689.1	0.0	0.88
S(.) p(state) Ψ(state)	13	694.2	5.1	0.07
S(state) p(state) Ψ(state)	15	696.2	7.1	0.03
S(state) p(.) Ψ(state)	15	696.8	7.7	0.02
S(.) p(.) Ψ(.)	3	3,414.7	2,725.6	0.00
B. Breeding probabilities for females ≥ 2 years old ($\hat{c}$ = 1.21)				
S(.) p(roost) Ψ(state)	9	1,253.3	0.0	0.91
S(.) p(state) Ψ(state)	5	1,258.6	5.3	0.06
S(state) p(state) Ψ(state)	6	1,260.7	7.3	0.02
S(.) p(state + roost) Ψ(state + roost)	25	1,324.0	70.7	0.00
S(state) p(state + roost) Ψ(state + roost)	26	1,325.2	71.9	0.00
S(roost) p(roost) Ψ(state + roost)	24	1,332.1	78.8	0.00
S(state + roost) p(state + roost) Ψ(state + roost)	36	1,348.4	95.1	0.00
S(year) p(year) Ψ(year)	9	1,369.0	115.7	0.00
S(.) p(roost) Ψ(.)	8	1,371.3	117.9	0.00
S(.) p(.) Ψ(.)	3	1,374.6	121.3	0.00
S(.) p(roost) Ψ(roost)	13	1,375.2	121.8	0.00
S(state) p(roost) Ψ(roost)	14	1,377.2	123.9	0.00
S(roost) p(roost) Ψ(roost)	18	1,384.6	131.3	0.00
S(state × roost × year) p(state × roost × year) Ψ(state × roost × year)	108	1,469.2	215.8	0.00
C. First year postweaning survival of females ($\hat{c}$ = 1.33)				
φ(age × roost × year) p(roost)	43	1,670.1	0.0	0.92
φ(age × roost + year) p(roost)	19	1,674.9	4.8	0.08
φ(age × roost) p(roost)	15	1,687.4	17.3	0.00
φ(age × year) p(roost)	13	1,690.6	20.4	0.00
φ(roost) p(roost)	10	1,691.6	21.5	0.00
φ(age) p(age)	4	1,697.8	27.7	0.00
φ(age) p(year)	6	1,701.4	31.3	0.00
φ(year) p(year)	7	1,701.8	31.7	0.00
φ(age) p(roost)	7	1,702.1	32.0	0.00
φ(year) p(roost)	9	1,704.1	34.0	0.00
φ(.) p(.)	2	1,709.0	38.8	0.00
φ(.) p(year)	5	1,714.7	44.6	0.00
φ(age × roost × year) p(age × roost × year)	68	1,714.9	44.7	0.00