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Survival Estimation in Bats: Historical Overview, Critical Appraisal, and Suggestions for New Approaches

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There are more than 1,100 species of bats, representing nearly 20% of all species of mammals (Simmons, in press). Bats occur on every continent except Antarctica, and although they occur in greatest diversity in the tropics, their distribution extends at least to tree line at high latitudes. Given this wide distribution and high species richness, it is not surprising that bats display a large number of feeding specializations and play key functional roles in ecosystems. Insectivorous bats are best known to temperate zone biologists, but at lower latitudes other species are frugivorous, nectarivorous, piscivorous, carnivorous, or even sanguivorous (blood-feeders). Bats play important ecological roles as pollinators and dispersers of fruit seeds in warm climates and as major consumers of insects in most terrestrial ecosystems. These attributes are of significant economic and ecological benefit, but some bats can also be detrimental to human affairs. In the neotropics vampire bats negatively affect livestock health, and bats may play an as yet poorly understood role in disease transmission cycles.

In light of their importance, bats are also of global conservation concern. Many species of bats are endangered or are considered "sensitive" species in the United States, and several nations provide legal protection to bats. Negative impacts on bat populations have stemmed from a variety of factors. These include habitat loss, declines in roost availability, disturbance to

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roosts (especially at winter hibernacula in caves), intentional killing of bats in vulnerable aggregations, hunting for food (particularly Old World fruit bats), and mortality due to environmental contaminants.

Considering the high diversity, wide distribution, ecological significance, economic importance, and conservation issues of bats, surprisingly little attention has been given to the application of modern approaches toward understanding their population biology. This is particularly true for estimation of survival. Some of this inattention has been a result of logistic difficulties. Most species of bats are difficult to observe because they are active at night and roost during the day in secretive or inaccessible places. All bats fly and thus can be highly mobile. However, cryptic behavior, mobility, and logistic difficulties are common to many of the other problematic groups of animals that are discussed in this book. The lack of detailed information on survival in bats may also be in part due to past lack of widespread recognition of their importance, particularly in comparison with other groups of mammals such as large herbivores, marine mammals, and economically important predators, furbearers, and crop pests. In addition to logistic challenges, thorough study of the population biology of bats can require a long-term commitment. Bats are long-lived for mammals of their size and reproduce slowly. Maximum longevity of several species of bats of temperate zones have been documented at more than 25 years (e.g., Ransome 1995; Keen and Hitchcock 1980) and in some cases at more than 30 years (reviewed by Barclay and Harder 2003). Bats typically give birth to single young (or much less frequently twins) just once annually (Tuttle and Stevenson 1982).

Our objectives in this chapter are to provide an overview of past sampling aimed at estimation of survival in bats, a parameter critical to understanding their population biology. We then point out some of the deficiencies of past work in comparison with the potentially more reliable inferences that may be possible through the application of new and powerful tools that are rapidly developing for the analysis of survival in wildlife populations. In highlighting deficiencies we do not cast aspersions on past efforts. In most cases these investigations provided very hard-earned results; they were as thorough and allowed as much inference as was possible given the limitations of the methods available. Instead we seek to emphasize to researchers the potential benefits of taking new directions using techniques that have only recently become practical for application to bats. We provide examples of such approaches from the recent literature and from our own nascent work on big brown bats (*Eptesicus*

fuscus) in Colorado. We hope this review will serve not only to stimulate bat biologists to consider new approaches in their studies of survival, but also to stimulate thought toward designing new applications for sampling this intriguing group of mammals.

Bat Banding

Past research on bat survival relied heavily on banding for marking of individuals. We therefore provide an overview of the history and range of findings from bat-banding studies, emphasizing those in the United States.

History and Overview of Banding Studies in Bats

Allen (1921) first applied bands to bats. He placed numbered aluminum bird bands on the legs of four female eastern pipistrelles (*Pipistrellus subflavus*) from a roost at a residence in Ithaca, New York in 1916. He recovered three of the banded bats at the same location in 1919. A second study was completed soon thereafter, documenting returns of banded *Eptesicus fuscus* in California (Howell and Little 1924). Allen (1921:55) noted, "The valuable results that are now being obtained by banding birds could no doubt be duplicated with bats if only enough persons would cooperate in the project of banding."

Banding of bats did indeed grow over the next half-century. Managing and coordinating bat banding was an official function within the U.S. Fish and Wildlife Service (USFWS) beginning in 1932, but it had no legislative mandate and the work never achieved a scale comparable to that of banding birds. From the 1930s through the mid-1960s, the USFWS and its predecessors issued about 1.5 million numbered metal bands for placement on bats (Greenhall and Paradiso 1968; estimated at 1.9 million by 1982 in Hill and Smith 1984). Banding of bats in the United States grew slowly in the 1930s (Mohr 1952) but intensified during the 1950s and 1960s. Most banding efforts were aimed at local or regional studies carried out independently by field biologists, particularly those interested in bats that use caves (Mohr 1952; Greenhall and Paradiso 1968). Modifications to design and techniques were made during this period (Barclay and Bell 1988; Greenhall and Paradiso 1968). Banding also took place in at least 14 European nations, Mexico, Japan, and Australia, involving additional hundreds of thousands of bats (Greenhall and Paradiso 1968; Hill and Smith 1984; Kuramoto et al. 1985).

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Banding provided previously unattainable information on the natural history of bats. In addition to investigations of survival, recaptures of banded individuals revealed patterns in reproduction (Pearson et al. 1952), migration (see below), longevity (Ransome 1995; Keen and Hitchcock 1980), growth (see review by Tuttle and Stevenson 1982), energetics and physiology (Kurta et al. 1989, 1990), and aspects of behavior such as site fidelity (Rice 1957; Tinkle and Patterson 1965), social organization (Dwyer 1970; Bradbury and Vehrencamp 1976), and homing (Davis 1966a; Wilson and Findley 1972). A prime example of discoveries made about bat migrations stems from banding of Mexican free-tailed bats (*Tadarida brasiliensis mexicana*). These bats form huge colonies in the southwestern United States that are the largest aggregations of mammals on Earth. Banding allowed discovery of seasonal migrations between these locations and Mexico, with documentation of some stopover points and movements among caves (Constantine 1967; Cockrum 1969; Glass 1982). Recovery of banded Mexican free-tailed bats was low, but outlines of migratory patterns emerged from compilations of anecdotal case records. Cockrum (1969) reported banding 162,892 free-tailed bats at 71 localities in Arizona and adjacent regions during 1952–1967. Only 539 (0.3%) were recovered at locations other than the point of banding (just 3,240 [2%] were recovered at the original banding sites), and nearly all of these were recaptured just once. Nonetheless, one-way migratory journeys of 1,600–1,800 km were documented (Villa-R. and Cockrum 1962; Constantine 1967; Cockrum 1969; Glass 1982). Serendipitous recoveries of a few bats in migration revealed travel rates of at least 64 km per night. Banding records of this species also showed complex geographic patterns in migratory tendencies in the western United States (Cockrum 1969) that prompted speculation about genetic distinctiveness in these areas. Such distinctiveness was not born out by subsequent genetic studies (McCracken et al. 1994; McCracken and Gassel 1997; Svoboda et al. 1985).

Findings from banding studies also documented other aspects of natural history, the annual cycle of reproduction and movements, and regional migrations to hibernacula of bats in the eastern United States, particularly in New England and New York (Griffin 1945). Davis and Hitchcock (1965) banded about 71,000 little brown bats (*Myotis lucifugus*) in this region. They noted movements between hibernacula and nurseries of up to 320 km and rates of travel of at least 43 km per night. Banding studies also showed that in certain locations, some species of bats make only local seasonal movements (e.g., *Corynorhinus townsendii*, Pearson et al. 1952,

Humphrey and Kunz 1976; *Macrotus waterhousii*, Cockrum et al. 1996). Banding studies also provided information on seasonal migrations of European bats over various distances, ranging from local movements (e.g., 1–64 km; Hooper 1983) to longer distances (e.g., 250–300 km in *Myotis dasycneme*; Sluiter et al. 1971). Distances of movements away from banding localities ranging up to 120 km were recorded for several species of bats in Japan (Kuramoto et al. 1985), and Dwyer (1966) reported complex seasonal movement patterns of nearly 600 km for banded *Miniopterus schreibersii* in Australia.

Critical Appraisal of Bat Banding

Although much was learned about the natural history of bats from banding studies, the technique poses problems. Chief among these are injuries and infections from banding, and obliteration of numbers on bands by chewing or by overgrowth of tissues on the forearm (bat biologists switched from banding legs to using wing bands in the late 1930s [Trapido and Crowe 1946]). These problems varied by species, with some more sensitive than others. Among U.S. bats, *Corynorhinus townsendii*, for example, was reported to be very sensitive to injury from bands (Humphrey and Kunz 1976), whereas *Pipistrellus subflavus* was not thought to be sensitive (Davis 1966b). Partial rectification was sought by shifting from bird bands to a lipped design made specifically for bats based on modifications developed by a few European bat banders (Hitchcock 1957), but injuries continued to be reported. About 42% of the Mexican free-tailed bats tagged with bird bands had visible irritation, wing tears, embedding in bone, or fleshy outgrowths with evidence of infection by about 300 days post-banding; 73% of those tagged with lipped bat bands had injuries, although these were described as less severe than those caused by bird bands (Herreid et al. 1960). Skeletal damage also occurred (Perry and Beckett 1966). In contrast, Happold and Happold (1998) reported less injury in *Pipistrellus nanus* marked with lipped bands in Malawi and concluded that the effects were not serious. Injuries to wings due to banding were also apparent from studies of some European bats (e.g., Sluiter et al. 1971).

In Australia, Baker et al. (2001) provided perhaps the most thorough documentation of injurious effects of bands on bats. Their records and analyses showed that injury rates and severity varied with species (17 species of insectivorous bats were banded with different types of bands and recaptured over multiple years), person applying bands, band type (bird

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bands were less injurious to some species than bat bands), band material, and size of band (Baker et al. 2001). Bats also may suffer marked premature tooth wear from chewing at bands (Young 2001), which could result in shortened longevity.

In addition to direct injury, much of the banding of bats in the United States and Europe took place at winter hibernacula in caves or mines (Mohr 1952). The energetic cost of arousal from hibernation due to disturbance (that is, banding activities) can be extreme. The amount of energy mobilized from fat for a single arousal can cost as much as 68 days of the supply a bat needs for hibernation (Thomas et al. 1990). Thus, bats disturbed during hibernation for banding have a reduced capability of surviving over winter and lower prospects of countering starvation if faced with food shortages during uncertain spring conditions. Banding of bats at hibernacula very likely drove population declines of bats at some sites in the United States (e.g., Tinkle and Patterson 1965; Keen and Hitchcock 1980). Daan (1980) suggested that marked declines in counts of six of eight species of bats in 16 limestone caves in The Netherlands during 1940–1979 also were likely a result of banding, perhaps due to very high adult mortality. Daan (1980:101) noted that banding as a source of mortality “is certainly serious enough to affect the conclusions obtained with the technique.”

In the United States, attitudes moved from a formal resolution of the American Society of Mammalogists in favor of bat banding in 1964 (Greenhall and Paradiso 1968) to an official policy to cease issuing of bat bands by the USFWS in 1973, primarily because of disturbance (Jones 1976). Similarly, Australia began an official bat banding program in 1960 (Young 2001). Subsequently, a permanent moratorium on banding eastern horseshoe bats (*Rhinolophus megaphyllus*) was instituted in Australia in the 1970s following recognition that up to 88% of banded bats had moderate to severe injuries (Young 2001). In 1996 Australia extended the moratorium on banding to all microchiropteran bats in three families (Baker et al. 2001). Recommendations to curtail banding also were made in Europe (e.g., Rybar 1973; Hooper 1983).

Suggestions for Future Studies

Biologists continue to band bats for various purposes. The use of bat bands in studies of survival should be eschewed unless investigators can empirically determine that resulting injuries and biases are very minor. Further research is needed on alternative methods of permanently marking bats.

Barclay and Bell (1988) list a number of possible alternatives. Necklaces and ear tags have been used on bats (Appendix 15.1; Mohr 1952). However, injuries can result from necklaces (Barclay and Bell 1988) and ears have very critical functions in orientation and prey detection. Tag loss also may be a problem with these methods. Necklaces were lost in five of 73 (6.8%) doubly marked (bands and necklaces) Jamaican fruit bats, *Artibeus jamaicensis* (Gardner et al. 1991) and in 6.5% of short-tailed fruit bats, *Carollia perspicillata* (Fleming 1988). Loss of ear tags also has been reported (Hoyle et al. 2001). Freeze-branding is another possible method of permanent marking that has only recently been explored in bats (Sherwin et al. 2002).

Participants at a 1999 workshop on monitoring bat populations recommended exploring various potential new marking techniques such as microtaggants and passive integrated transponders (PIT tags) (Working Group A report in O'Shea and Bogan 2003). PIT tags are small (ca. 0.1 g, 11 mm length), long-lasting implant devices that have been extensively used in fisheries and to identify pets. They are passive, and instantaneously emit a unique binary ultrasonic code only when activated and simultaneously received by reader devices at very close range. PIT tags have been used to mark big brown bats in captivity (Barnard 1989) and in field studies of activity patterns, social structure, and genetics of a few species of bats (Brooke 1997; Horn 1998; Kerth et al. 2002). They have not yet been applied to estimation of survival in bats, although we provide a case example below that suggests some promise. There also is a need for a clearinghouse for information about such techniques and to coordinate contacts for ongoing studies of marked bats (e.g., when remote recoveries are made), including banding studies (Working Group C report in O'Shea and Bogan 2003).

Estimation of Survival

There have been two previous reviews of the study of survival in bats. Keen (1988) provided a critical appraisal of the literature through 1984, and Tuttle and Stevenson (1982) reviewed those studies appearing through 1982. Here we provide an updated chronological review, critique, and suggestions for future approaches.

History and Overview of Survival Studies in Bats

We surveyed the literature on survival estimation in bats published since 1950 (Appendix 15.1). We found 42 studies with information relevant to

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estimating survival in 36 species of bats in the Americas, Europe, Asia, and Australia. Earlier efforts in the 1930s and 1940s (summarized by Mohr 1952) simply expressed the percentage of banded bats recaptured at sites where originally banded. To our knowledge, the first published attempts at calculating survival estimates for bats were those of Beer (1955) for hibernating big brown bats in Minnesota (Appendix 15.1). As pointed out by Keen (1988), these estimates were based on an incorrect application of Hickey's (1952) ad hoc (Williams et al. 2002) procedures for estimating survival from recoveries of bands from dead birds.

Soon afterward, a series of papers appeared based on banding of thousands of bats of several species at winter hibernacula in The Netherlands over many years. This work provided survival estimates based on the "method of Bezem" (Sluiter et al. 1971:7; Sluiter et al. 1956; Bezem et al. 1960). This was a life table approach that pooled recaptures of unaged cohorts. Bezem's technique involved calculating the proportion of bats caught in any one year out of those bats caught the previous year, and plotting the logarithm of the proportion against the number of years since banding. Under unlikely assumptions of constant rates of survival and constant capture probabilities, the coefficient of regression of a straight line fitted to these points was taken as the annual survival estimate for the study period and the y-intercept was taken as the capture probability. Sluiter et al. (1956) gave a detailed mathematical rationale for this approach and provided justification via simulation. They acknowledged drawbacks to their methods and assumptions but noted that without using the regression technique, "the computational labour [for estimating annual survival and capture probabilities] rapidly becomes enormous as the number of years increases" and "therefore we have turned to a method which, though it may lead to slightly erroneous results, has the advantage that the necessary calculations are very easy" (Sluiter et al. 1956:74). This work was done a half-century ago when this justification was perhaps understandable.

Bezem's approach (with modifications), coupled with life table analyses derived from the slopes of the regression lines under an assumption of constant survival, prevailed in survival estimation in bats for the next 30 years (Appendix 15.1). This was despite the appearance of Cormack's (1964) paper and others on maximum-likelihood-based methods, the increasing availability of electronic computing techniques, and the specific rejection by Caughley (1966) of the assumptions (particularly constant rate of survival) made by Bezem. Maximum-likelihood methods, intro-

duced by R. A. Fisher (1922), provide the means for estimating parameters from sample data given an appropriate model and are “the backbone of statistical inference used in nearly every area of science” (White 2001:37). For descriptions of properties and methods of maximum-likelihood estimation, particularly as they relate to capture-recapture models, see White et al. (1982), Burnham and Anderson (2002), and Williams et al. (2002).

Studies that relied on regression varied in their methods of computations of the proportions that formed the regression points, which in some studies are not clearly specified. Bezem and coworkers (1960) included all observations of any banded bat 1 year apart as survival 1 year after marking; thus, each banded bat could be counted several times in the estimate of each regression point (Keen 1988). The “intuitive regression” (Keen 1988:167) method employed by most workers used a minimum-number-known-alive (MNA) approach in calculating the proportions in the regression points (a bat not seen between successive captures was calculated as present or alive at the intervening periods when it was not captured). Some studies made study-specific modifications to computations; for example, Davis (1966a) used an ad hoc computation to correct percentage recaptured by the estimated number alive but not recaptured. However, justification for the form of the correction was not provided and properties such as bias were unknown. Data used for both Bezem’s and the intuitive regression methods were not appropriate for regression because they were not statistically independent (Keen 1988).

Of the 42 studies of bats we reviewed (Appendix 15.1), 7 (17%) used the maximum-likelihood-based Cormack-Jolly-Seber (CJS) model to estimate survival of bats, whereas 35 (83%) used ad hoc methods. The CJS model is a preferred, maximum-likelihood method based on open populations that allows estimation of survival and capture probabilities, and conditions on the capture, marking, and release of individuals at each of several times during a study (Williams et al. 2002). The ad hoc methods included simple reporting of recapture percentages by time period (about 20% of all studies); some form of “intuitive regression,” often on pooled unaged cohorts with life tables derived by assuming constant rates of survival (about 50%); life tables of known age cohorts (2%); and other ad hoc methods (about 13%). Accordingly, estimates of variance for survival rates were made only in a small number of cases. A few studies used combinations of analytical approaches (e.g., Boyd and Stebbings 1989; Fleming 1988; Keen and Hitchcock 1980). Most studies of survival in bats were primarily

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descriptive reporting of estimates (about 76%); a few studies involved statistical null hypothesis testing, usually regarding sex (Appendix 15.1). These generally involved tests of differences in slopes of the regression lines or χ^2 tests of proportions recaptured at various time periods in age and sex categories.

Application of more useful modern approaches to estimating survival in bats occurred in two phases: (1) the first CJS-based estimates of survival appeared during 1980–1990 (Keen and Hitchcock 1980; Hitchcock et al. 1984; Boyd and Stebbings 1989; Gerell and Lundberg 1990); and (2) three very recent studies that used CJS estimators to evaluate specific hypotheses about survival in bats in Australia and Germany. Baker et al. (2001) reported that survival estimates of banded bats varied by type of band in *Nyctophilus geoffroyi* but not in two other species of Australian bats. Hoyle et al. (2001) adopted the information-theoretic approach (Burnham and Anderson 2002) to model selection and evaluated biological hypotheses about survival in the large Australian ghost bat, *Macroderma gigas*. The preferred model included sex, season, and rainfall as factors or covariates influencing survival in this species (Hoyle et al. 2001). Sendor and Simon (2003) also used the information-theoretic approach to select models for the effects of age, time, sex, season, and winter severity on annual survival in pipistrelles (*Pipistrellus pipistrellus*) captured with mist nets and banded at a site in Germany that was used both as a hibernaculum and in summer. Based on the most parsimonious models, age had the strongest effect on survival in the pipistrelles: survival was lower in bats in their first year than in adults. No differences in survival of the sexes were apparent, and there was no effect of winter severity, time, or season on survival.

Although methods to estimate survival from most past studies had flaws, some generalizations about the life history of bats emerged from these efforts. Survival and longevity are higher in bats than in most other mammals of similar size, and survival through the first year of life (or first year of banding in unaged cohorts) is usually lower than in subsequent years. Survival estimates for juvenile male bats often seem lower than in juvenile females, but this may in part be due to emigration and differential dispersal from natal roosts. It is difficult to draw many other reliable conclusions about survival in bats; accuracy and precision of most estimates are unknown, despite the tremendous efforts that have been involved in acquiring past recapture data.

Critical Appraisal of Survival Studies in Bats

Most previous studies of survival in bats suffer from shortcomings in at least one of three areas. The first of these was failure to specify the population of interest, or target population (defined in sampling theory as a collection of elements about which we wish to make inferences; Cochran 1977; Scheaffer et al. 1986), and to employ a sampling design that allows valid inferences to be made from the sample population (a collection of sample units drawn from a sample frame; Cochran 1977, Scheaffer et al. 1986) to the target population. For example, some study sites were likely chosen on the basis of convenience sampling (Anderson 2001:1294), where locations were based on prior knowledge that certain sites had bats and perhaps were closer to the researchers or less difficult to work in than others. This was not problematic insofar as the investigator limited inferences to the study sites actually sampled (assuming appropriate sampling at the sites). However, in past studies survival estimates were sometimes taken to apply to some larger population or even the entire species. A related problem was that much of the past estimation of survival was based on studies in which banding may have been carried out with multiple objectives (such as determining ranges of movements) and marking was not designed specifically for survival estimation. Consequently, the sample population was not representative of the target population, and this prevented valid inferences about survival.

A second shortcoming was the use of field methods that reduced survival in the sample population so it was no longer representative of the target population or that introduced biases of unknown magnitude into the sample data. For example, potentially injurious banding was used in 34 of the 36 studies that involved marked bats (Appendix 15.1), and 17 (40%) of the 42 studies estimated survival but involved sampling bats in hibernacula where disturbance-induced arousals can be a major source of overwinter mortality (11 of the 16 [68%] studies of marked bats in the United States and Canada involved sampling at hibernacula). Thus, the majority of survival studies based on recaptures of bats used field methods known or suspected to cause injury and reduced survival in marked individuals. Consequently, survival estimates for marked individuals in these studies could not represent survival rates for the unmarked portion of the population. Other sources of bias in the sample data included effects due to tag loss, inconsistent sampling efforts, and heterogeneity in responses to past cap-

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ture and handling. Tag loss problems include effective tag loss, in cases where numbers on bands are obliterated from chewing or overgrowth of tissues on the forearm, or physical tag loss. Physical tag loss has also been reported for the two alternative marking methods (necklaces and ear tags) employed thus far (Gardner et al. 1991; Fleming 1988; Hoyle et al. 2001). The end result of tag loss was that, on average, fewer recoveries were likely recorded than actually occurred, and this likely biased survival estimates negatively. Stevenson and Tuttle (1981) pointed out other sources of bias from field methods in studies of survival in bats. These included unequal effort at recapturing bats among years and locations; widely varying characteristics of roosts and locations of bats within roosts that affected accessibility and capture probabilities; and differential segregation and accessibility of age and sex classes at capture sites. Individuals of some species of bats also have been shown to avoid recapture within hibernacula based on their experience from captures in previous years (Stevenson and Tuttle 1981).

The third shortcoming of many of the bat studies we surveyed was the use of ad hoc procedures for estimating survival, many of which invoked biologically unrealistic assumptions (such as constant rates of survival, despite year-to-year environmental stochasticity) or failed to state their assumptions. This included the use of life table approaches (Appendix 15.1), which are now considered ad hoc and circular (Anderson et al. 1981; Williams et al. 2002). Ad hoc estimators of survival are undesirable for the simple reason that they have no underlying theoretical justification or probabilistic framework in which to derive variance estimators or to evaluate important properties such as unbiasedness, efficiency, or consistency. Consequently, it is unknown if the calculated quantity is actually estimating the parameter of interest or if it is better in some sense than other ad hoc procedures. This leads to the problem described in Tuttle and Stevenson (1982:122) that "The student of chiropteran survival analyses will be considerably frustrated in attempting to compare the results of various studies." Obstacles to comparison occur because different estimators may be estimating different quantities and have no associated measures of precision.

Suggestions for Future Studies of Survival in Bats

Future research should avoid the shortcomings so prevalent in past studies. As a starting point, investigators must strive to clearly define their population of interest and then make every effort to construct an appropriate sample frame (a complete list of sample units; Thompson et al.

1998). In some cases it may not be possible to construct a sample frame that exactly matches the target population. For example, if an investigator wishes to make inferences about the population of bats that roosts in a particular geographic area (the target population), then he or she must first locate all the roosts in that area so as to choose a probability sample from that population. However, in constructing the sample frame, some roosts may be missed because they contain few bats, whereas roosts containing large numbers of bats will be less likely to be missed. In such cases, the sample frame will be a size-biased representation of the target population and inferences drawn from a sample of roosts will be applicable only to roosts in the sample frame, not to the population of roosts in the geographic area of interest.

Once an appropriate sample frame has been developed, well-established sampling procedures such as simple random sampling, stratified random sampling, or perhaps cluster sampling should be used to select the sample population. In the example above, one might first stratify roosts on the basis of size and then select a simple random sample of roosts from each stratum. Of course, once a roost has been selected for sampling, it is desirable to obtain a representative sample of individuals from each roost. This can sometimes be difficult to accomplish for bats, though certain measures can be taken to minimize potential biases. For instance, one might ensure that capture efforts are distributed equally among all parts of a roost (e.g., a cave) rather than just the most accessible parts. If there are multiple exits from a roost, one might attempt to capture individuals at all of these exits instead of just a single exit.

Methods used to acquire and mark individuals must be improved. Using bands to mark bats for survival studies is unacceptable without empirical determination of the effects of bands on the species or situation of interest, nor is it acceptable to disturb bats on a large scale in hibernacula to mark individuals or acquire recapture information. Alternative marking techniques need to be developed that allow permanent identification of individuals without causing injury and potentially biasing estimates (see above section on banding; preliminary results from application of PIT tags as a marking alternative are provided in the case study described below). In addition, marking efforts should be applied away from hibernacula to avoid the effects of disturbance-induced arousals on overwinter survival and should instead focus at alternative locations where bats occur in summer or at the mouths of caves during swarming in autumn prior to hibernation. Improved methods of acquisition and marking that do not reduce

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survival of the sample population or introduce biases into the sample data will yield more informative and reliable estimates of survival that can be more confidently applied to the unmarked portion of the population.

Our final suggestion is to abandon the ad hoc procedures used in past studies to estimate survival. Inferior approaches should not be followed simply as a legacy of precedent. Instead, we recommend that survival estimators be based on well-founded probabilistic models and a sound theoretical foundation, such as maximum likelihood theory, and that assumptions upon which models are built be stated explicitly. In particular, we believe the CJS open population capture-recapture model shows great promise for estimating survival in bats, as previously stressed by Keen (1988). This likelihood-based model conditions on first captures, allows inferences to be made to the marked population, and is based on the following assumptions (from Williams et al. 2002:422):

(1) every marked animal present in the population at sampling period i has the same probability p_i of being recaptured or resighted; (2) every marked animal present in the population immediately following sampling in period i has the same probability ϕ_i of survival until sampling period $i+1$; (3) marks are neither lost nor overlooked and are recorded correctly; (4) sampling periods are instantaneous (or in reality they are very short periods), and recaptured animals are released immediately; (5) all emigration from the sampled area is permanent; and (6) the fate of each marked animal with respect to capture and survival probability is independent of the fate of any other animal (see Williams et al. 2002:422–423 for a discussion of these assumptions and consequences of their violation).

Generalizations to the CJS model allow survival, capture, and transition-state probabilities to be modeled as functions of individual or group covariates, and powerful software exists for estimating parameters under user-defined models (White and Burnham 1999). Transition-state probabilities are computed based on generalized CJS models that allow individuals to be distributed across multiple sites or phenotypic states, under the assumption that transitions among states follow a stochastic Markovian process (Williams et al. 2002). Furthermore, because the CJS model and its generalizations are likelihood based, the weight of evidence in favor of or against a particular candidate model can easily be evaluated using information-theoretic model selection procedures (Burnham and Anderson 2002). We anticipate that application of the CJS model in future bat studies will allow

for more rapid advances in understanding bat population biology and in application of findings for management.

Big Brown Bats in Fort Collins: A Case Study Combining New Approaches

In 2001 we began a study of the ecology of rabies transmission in big brown bats that roost in human-occupied buildings in Fort Collins, Colorado. One facet of the study was to estimate survival and transition-state probabilities of marked bats as they related to exposure to rabies. Rabies is transmitted through biting. In addition to determining the influence of rabies exposure and other factors on survival of bats, understanding rabies transmission dynamics in our study population also required an understanding of various transition-state probabilities that may influence possible contact among bats. Transition states may include movements of bats among roosts, shifts in exposure histories and immune status of bats based on serology, or transitions from noninfective to infective (virus shedding) phases.

Our study differed from most previous efforts to estimate survival, capture, and transition-state probabilities by combining several different marking, recapture, and analytical approaches. We employed a PIT tag method of marking bats rather than bands, we studied bats at maternity colonies rather than hibernacula, and we “resighted” bats using passive PIT tag readers placed at roost entrances rather than repeatedly capturing and handling bats to read tags. Our objective was to evaluate a number of hypotheses about survival and transition-state probabilities using a generalized CJS model (after Lebreton et al. 1992). Specifically, we developed competing models for survival, capture, or transition-state probabilities and then obtained the maximum-likelihood estimates for these parameters. Models were constructed a priori to evaluate the influence of select categorical variables and individual covariates of likely biological importance, such as age, sex, time, body condition, ectoparasite burdens, and ecological aspects of principal roosting sites. We used the information-theoretic approach (Burnham and Anderson 2002) to rank and select among competing models (hypotheses). In this section we provide results from three examples of our preliminary studies that involved estimation of short-term survival, capture, and movement probabilities of bats. Results cover only 2 years of marking and recapture (2001–2002), so

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findings regarding longer term annual estimates based on these approaches are not yet available.

Methods Employed in the Fort Collins Study

The study of big brown bats in Fort Collins involved selection of roosts for sampling without prior knowledge of roost locations, uniquely marking individuals using technology not previously applied to studies of survival in bats, and using maximum-likelihood-based analytical methods. This work attempted to address some (but not all) of the deficiencies identified in many of the earlier studies of survival in bats.

SELECTION OF ROOSTS FOR SAMPLING

Nearly all records of public exposure to rabid bats in Colorado are from encounters in and around buildings and parks in towns during summer (Pape et al. 1999). Therefore, we focused our sampling on summer maternity colonies (adult females and juveniles, adult males are widely dispersed) in buildings in Fort Collins (Figure 15.1). Selection of colony sites was not truly random. We located roosts for sampling by first capturing bats in mist nets at night as they flew over water for foraging or drinking in parks and open spaces. Thus individuals caught for tagging were probably encountered haphazardly. We then radio-tagged adult females and released them on site and drove the streets during the day to find colonies by tracking radio signals. For a more representative sample of bats, we also intentionally selected initial capture sites so that we included sections of the city spanning a range of ages of buildings. We radio-tagged 122 bats during summers 2001–2002 and located 54 buildings with colonies of at least 20 bats (some were occupied by bats for only a few days). Within this sample frame, we chose roosts for PIT tagging and biological sampling based on logistic considerations (equipment limitations, accessibility, potential cooperation). We also included a few colony sites in this total of 54 based on citizen knowledge. However, we did not select colony sites based on our own prior knowledge, and this differed from most previous studies of survival of bats.

CAPTURING, MARKING, AND RESIGHTING BATS AT ROOSTS

We captured bats as they exited from roosts at evening emergence, and thus captured only adults and volant juveniles (juveniles born that summer but probably at least 30 days old). In our examples below we did not

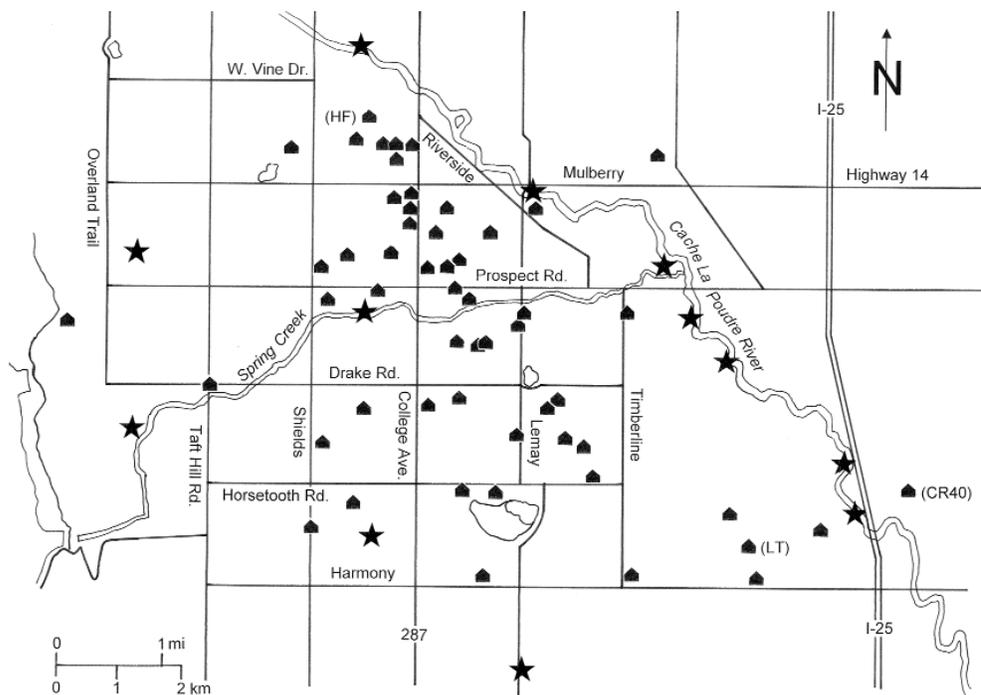


Figure 15.1. Fort Collins, Colorado, where big brown bats were sampled as part of a study of the ecology of rabies transmission in urban bats. Each square represents a one-square-mile section (2.6 km^2) of developed land in the city (population 120,000 people) bounded by major thoroughfares. Building symbols denote locations of structures used as roosts by big brown bats in 2001 and 2002, as discovered by radio-tracking adult females captured while foraging in parks and open spaces (capture locations denoted by stars). Abbreviations (LT, HF, CR40) correspond to specific roosts mentioned in tables and text of this chapter.

disturb bats by attempting to capture them within roosts. We used standard techniques and equipment for capturing flying or emerging bats, as described in detail in other sources (Greenhall and Paradiso 1968; Kunz and Kurta 1988; Kunz et al. 1996). Depending on locations of the exit points, we caught bats in harp traps (approximately $2 \times 2 \text{ m}$ frames with taut, closely spaced fine monofilament lines that flying bats collided with, then fell to collecting receptacles below) or in mist nets set on poles if exits were up to 5 m above ground. We captured exiting bats in mist nets suspended by pulleys from heights of 5–10 m in cases where exit points were high on the sides of buildings. We sometimes supplemented these with

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handheld nets and with funnel traps (custom-made, enclosed nylon tubes up to 10 m in length extending to the ground, see Kunz and Kurta 1988) placed over roost entrances.

We transported bats to the laboratory (isolated from each other in individual cotton specimen bags placed in disposable drink cups with lids) for biological sampling and for marking by subdermal injection of PIT tags. We followed transport, marking, and biological sample collection procedures described by Wimsatt et al. (in press) and then released the marked bats near the roost within 6 hours of capture. We PIT tagged 2,073 big brown bats at multiple sites in Fort Collins during 2001–2002. In 2002 we also marked newly PIT-tagged bats with small (3 mm diameter) circular freeze-brands over the left scapula. These spots were expected to grow out as small tufts of white pelage in the late summer moult (Sherwin et al. 2002). By August 2003 we reexamined 185 bats recaptured with white hair tufts, and just three lacked functional PIT tags (1.6%), suggesting that PIT tag loss was not a major problem.

In 2002 we installed 19 PIT readers at roosts in 14 different buildings. PIT readers are 15 or 30 cm diameter activating and receiving hoops that are each connected to a separate data logger and powered by 12 V automotive batteries (we used readers and PIT tags manufactured by AVID, Inc., Norco, California). PIT readers were installed over crevice openings where bats typically crawled over them upon emerging or entering. Data loggers stored the date, time, and identification number for every detection, and these were downloaded to a laptop computer three times each week throughout the summer. Tens of thousands of records were reduced to daily presence/absence for short-term survival studies.

DATA ANALYSIS

We used Program MARK (White and Burnham 1999) to generate estimates for parameters of interest. Encounter history files were created that included a listing of each individual bat, coded for every time period as either a “1” (captured), or “0” (not captured). We modeled data sets as “live recaptures,” in which animals are reencountered only when recaptured alive on succeeding occasions. Two of our parameters of interest were capture probability (p , the conditional probability that a marked animal will be seen over a specified time interval given that it is alive and in the study population; Cormack 1964; Williams et al. 2002) and apparent survival (ϕ). Apparent survival cannot distinguish emigration from mortality, but is the probability that the animal is alive, remains on the study area, and is avail-

able for recapture (White and Burnham 1999). The identification of models followed the notation of Lebreton et al. (1992). For example, a model incorporating a group effect (such as age or reproductive status) on apparent survival and capture probabilities was coded as $\{\phi(g), p(g)\}$. A model including time effects on survival and capture probabilities was coded $\{\phi(t), p(t)\}$. We also calculated a 1-year return rate ($\hat{r} = [\text{number recaptured at time } t + 1] / [\text{number released at time } t]$) and confidence intervals based on simple binomial probability.

Example 1: Comparisons of Estimates from Conventional Captures vs. PIT Readers

We hypothesized that daily probabilities of capture would be higher and daily survival would be more precisely estimated using passive PIT readers placed at roost entrances than by using conventional methods of capturing bats to read marks by hand. Individual bats probably vary in their susceptibility to capture in nets and traps and may learn to avoid them. We predicted that survival estimates would be comparable using the two methods because CJS-based survival estimators are typically robust to heterogeneity in capture probabilities (Nichols and Pollock 1983). However, PIT readers can sample continuously whereas conventional captures must be conducted sparingly because of effort requirements, possible abandonment of roosts, and animal welfare considerations. Thus the larger number of samples obtainable by PIT readers should result in more precise estimates. We also predicted that estimates of overwinter return rates from 2001 to 2002 would be higher using reader records than estimates obtained by hand captures.

We created separate encounter history files for conventional captures and for PIT readers at roosts in three buildings. Conventional captures were conducted at least five times during summer 2002; PIT readers were operational over the intervals between first and last conventional captures at each of these three buildings. We analyzed samples separately by building because each differed in degree of difficulty in capturing bats. We did not use samples that occurred after mid-August because of postbreeding dispersal. We used Program MARK to adjust differing intervals between occasions and then converted these to daily rates. Capture events were typically 2 weeks apart (Table 15.1). We generated estimates of daily survival and capture probabilities for the two different techniques using a model incorporating age as a group effect (adult females and juveniles of both

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Table 15.1.

Daily capture probability (\hat{p}) and apparent survival estimates ($\hat{\phi}$) for big brown bats at three different roosts in Fort Collins, Colorado (see Figure 15.1), during the summer of 2002. Estimates were compared using conventional capture techniques (mist nets and traps, with tag reading during handling) and PIT reader records collected passively between the first and last conventional capture events.

Roost	Method (<i>n</i> occasions)	\hat{p} (95% CI)		$\hat{\phi}$ (95% CI)	
		Adults	Juveniles	Adults	Juveniles
HF ^a	Conventional captures (5)	0.091 (0.034–0.219)	0.064 (0.035–0.115)	0.974 (0.917–0.992)	Inestimable ^b
	PIT readers (30)	0.862 (0.851–0.872)	0.678 (0.637–0.716)	0.989 (0.987–0.991)	0.967 (0.955–0.976)
CR40 ^c	Conventional captures (5)	0.494 (0.365–0.623)	0.447 (0.221–0.697)	0.987 (0.975–0.993)	0.987 (0.975–0.993)
	PIT readers (30)	0.743 (0.717–0.768)	0.938 (0.876–0.970)	0.986 (0.980–0.990)	0.976 (0.948–0.989)
LT ^d	Conventional captures (5)	0.204 (0.115–0.335)	0.334 (0.158–0.572)	0.984 (0.954–0.994)	0.985 (0.874–0.998)
	PIT readers (21)	0.858 (0.842–0.872)	0.860 (0.806–0.900)	0.988 (0.984–0.991)	0.973 (0.954–0.985)

^a Conventional captures occurred on 14, 28 June, 12, 26 July, and 12 August 2002.

^b Incalculable due to low capture probability of juveniles during conventional captures.

^c Conventional captures occurred on 10, 24 June, 8, 22 July, and 8 August 2002.

^d Conventional captures occurred on 11, 26 June, 10, 24 July, and 6 August 2002.

sexes). (These daily survival rates should not be converted to estimate annual rates because sampling may have included early dispersal; differences in severity of seasonal mortality were also likely and these estimates were made only in summer.) Several PIT reader input files were truncated from daily encounters to encounters for every 48-hour period to allow the model to reach numerical convergence in Program MARK.

Capture probabilities at all three roosts (Table 15.1) were up to 10-fold higher when estimated from PIT readers than when estimated from conventional techniques. Capture probabilities also varied more widely among roosts for conventional captures than for PIT readers. The probability of capturing bats was highest at roost CR40 and lowest at HF. The CR40 roost opening was within 5 m of the ground and most bats that emerged to forage were easily captured, whereas emergence points at HF were less pre-

dictable and were located 10 m above ground. Estimates of apparent survival were similar but confidence intervals were more precise when estimates were derived from PIT readers in comparison with conventional captures (Table 15.1).

Return rates of females from 2001 to 2002 were high when bats were resighted by PIT readers, and most of these individuals were never detected using conventional methods. We PIT tagged 404 adult females at seven roosts during 2001 that were monitored by readers in 2002; 81.9% [95% CI = (78–86%), $n = 331$] returned in 2002. This is higher than most rates reported in the literature for this species based on other methods (Appendix 15.1). Return rates of juvenile females (103 of 163, or 63%; 95% CI = 56–70%) also were higher. Two hundred fifty-two of 434 (58%) bats of both age groups combined that were detected by PIT readers during 2002 were never recaptured by hand at roosts, despite multiple conventional captures to obtain biological samples and compare capture techniques.

Example 2: Effects of Biological Sampling Techniques on Survival

We used techniques developed and described by Wimsatt et al. (in press) to sample blood of anesthetized big brown bats to obtain serum for rabies antibody determination. Obtaining blood samples from large numbers of bats under anesthesia and releasing them in the field was not common in most studies of bats, and this was the most invasive aspect of our biological sampling. Therefore, in this example we summarize findings of Wimsatt et al. (in press), who sought to determine if these procedures affected short-term survival of big brown bats.

Wimsatt et al. (in press) used a random number table to randomly assign individuals captured by hand during summer 2002 to a treatment (handled and sampled for several biological attributes, anesthetized, and blood sampled through intravenous puncture) or a reference group (handled and sampled, but not anesthetized and no blood taken). Bats were held until all were processed and released simultaneously near their roosts each night when sampling was completed. We obtained daily PIT reader records at roosts where the readers were operational for 14 consecutive days after capture. Separate encounter history files were created for adults and juveniles. We sampled adult females from six roosts ($n = 179$ treatment, 86 reference group) and juveniles from five roosts ($n = 87$ treatment, 92 reference group). We estimated daily survival over the 2 weeks following the

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Table 15.2.

Maximum likelihood estimates of short-term apparent survival ($\hat{\phi}$) and capture probabilities (\hat{p}) for adult female and juvenile big brown bats by treatment (anesthetized and bled) and reference (not anesthetized, not bled) groups. Estimates were based on passive detection by PIT tag readers placed over roost entrances (see also Wimsatt et al., in press; reproduced with permission of the Journal of Wildlife Diseases).

Treatment	Adults		Juveniles	
	$\hat{\phi}$ (95 % CI)	\hat{p} (95 % CI)	$\hat{\phi}$ (95 % CI)	\hat{p} (95 % CI)
Anesthetized and bled	0.984 (0.977–0.989)	0.757 (0.738–0.775)	0.968 (0.954–0.978)	0.636 (0.604–0.668)
Not anesthetized, not bled	0.958 (0.942–0.978)	0.757 (0.725–0.785)	0.956 (0.940–0.968)	0.660 (0.626–0.692)

first capture, handling, and bleeding of the season (some individuals were bled more than once during the summer). We used Program MARK to estimate survival and capture probabilities for the two groups of bats and goodness-of-fit Test 1 in Program RELEASE (Burnham et al. 1987) to test for differences between the groups. We also attempted to assess possible longer term impacts of multiple sampling sessions by comparing return rates in 2002 of female bats (most males do not use maternity roosts) that had been captured, handled, and bled once or twice in 2001.

We did not detect a difference in 14-day daily survival and capture probabilities (Table 15.2; Wimsatt et al., in press) of bats that were sampled for blood under anesthesia and those that were not ($\chi^2 = 22.2, df = 27, P = 0.73$ for juveniles; $\chi^2 = 9.7, df = 18, P = 0.94$ for adults). Return rates in 2002 for bats bled once or twice during the summer of 2001 were high and confidence intervals overlapped widely with estimates of return rates for bats not bled in 2001 (Table 15.3). These results provide some assurance that the most invasive aspects of the biological sampling did not strongly bias our estimates of apparent survival.

Example 3: Feasibility of Using PIT Marking to Estimate Transition-State Probabilities

This third example was a preliminary study in which we had two objectives. Our first objective was to estimate daily probabilities of movement

Table 15.3.

First year (2001–2002) return rates (\hat{r}) for female big brown bats handled, but not anesthetized and bled, or sampled for blood under anesthesia once or twice during 2001 (after Wimsatt et al., in press; reproduced with permission of the Journal of Wildlife Diseases).

Age	Treatment		
	Not sampled	Sampled once	Sampled twice
Adults	58/72 $\hat{r} = 0.806$ $S\hat{E}(\hat{r}) = 0.0466$ 95% CI (0.698–0.881)	227/276 $\hat{r} = 0.822$ $S\hat{E}(\hat{r}) = 0.0230$ 95% CI (0.773–0.863)	42/50 $\hat{r} = 0.840$ $S\hat{E}(\hat{r}) = 0.0518$ 95% CI (0.711–0.918)
Juveniles	16/29 $\hat{r} = 0.552$ $S\hat{E}(\hat{r}) = 0.0924$ 95% CI (0.372–0.719)	75/113 $\hat{r} = 0.664$ $S\hat{E}(\hat{r}) = 0.0444$ 95% CI (0.572–0.745)	12/17 $\hat{r} = 0.706$ $S\hat{E}(\hat{r}) = 0.1105$ 95% CI (0.458–0.872)

based on PIT reader records. Our second objective was to use model selection procedures (Burnham and Anderson 2002) to evaluate a priori hypotheses about factors that may influence daily movements of bats among roosts.

Many studies using radio-tagging and other observational methods have shown that individuals of many species of bats (including big brown bats in maternity colonies) switch roosting sites from day to day (see Lewis 1995 for a review). However, probabilities and variances associated with such movements have never been estimated. Hypotheses in the literature suggest that movements of bats among roosts may be explained by a number of factors. Two prominent factors proposed to influence the probability of movement among roosts are day-to-day microclimatic shifts and ectoparasite infestations. To our knowledge, Lewis (1996) conducted the only field study that investigated the relative importance of these two possible explanations. Based on daily radio-tracking, she reported that individual pallid bats (*Antrozous pallidus*) with higher ectoparasite loads switched roosts more often (based on an ANOVA approach), but that changes in roost use did not appear to be in response to daily changes in temperature.

We used the model of Brownie et al. (1993) and Hestbeck et al. (1991), which generalized the CJS model to allow animals to move among multiple strata by modeling transition probabilities (ψ). To meet the first objective of this example we calculated ψ for members of a maternity colony of

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big brown bats that used four locations within one large building (HF); each location was monitored with a PIT tag reader at its opening. The locations were designated as northeast (NE), northwest (NW), southeast (SE), and southwest (SW). We assumed that bats roosted within walls near those locations. To meet the second objective we hypothesized that movement probabilities among these locations would be higher with more pronounced shifts in ambient temperature ranges. We also hypothesized that higher numbers of ectoparasites would increase movement probabilities.

We used multi-strata “live recaptures only” models in Program MARK to examine daily transition probabilities in relation to change in temperature the previous day (delta temperature [Δt], which we defined as the maximum temperature the previous day minus the minimum temperature that evening/morning) and total number of ectoparasites (mites of the genus *Steatonyssus*) counted on standard portions of the wings and body of each bat. We limited the analysis to those adult females captured in hand during 15–28 June 2002 at one stage of reproduction (lactation, $n = 43$; juveniles were not yet volant). We modeled number of ectoparasites as an individual covariate and Δt as an environmental covariate. The Δt spanned 11–23° C units over the 2-week period. Counts of ectoparasites ranged from 1 to 562 *Steatonyssus* sp. per bat [$\bar{X} = 130.6$ (SD = 156.5)]. We considered only models in which apparent survival was constant over the 2-week period. We estimated overdispersion (where sampling variance exceeds the theoretical, model-based variance; Burnham and Anderson 2002) by dividing the deviance of the most general model by its number of parameters. Deviance is the difference in $-2 \log$ (likelihood) of the current model and $-2 \log$ (likelihood) of the saturated model (the saturated model is the model with the number of parameters equal to the sample size; McCullagh and Nelder 1989; Lebreton et al. 1992). The most parsimonious models were selected using QAIC_c (Akaike’s Information Criterion corrected for overdispersed data) (Burnham and Anderson 2002).

Our results show that resightings from PIT readers in nearby alternative roosting locations can be used in multi-strata models to estimate movement probabilities and to model associated environmental and individual covariates (Tables 15.4 and 15.5). Estimated movement rates from the north to the south (that is, NE to SE and NW to SE) were generally higher over the period of analysis than movements from the south to the north (that is, SE to NE and SE to NW; Table 15.4). Estimated movement rates also were generally higher from the north to the south than between points on the same side of the building (that is, NE to NW and NW to NE). Movement rates

Table 15.4.

Estimates of transition probabilities ($\hat{\psi}$) and corresponding 95% confidence intervals for female, lactating big brown bats during 15–28 June 2002 at the HF building, Fort Collins, Colorado. NE, NW, SE, SW were the four strata (roost locations) used. Model { p All (.), ψ All (.)} was used to estimate probability of transitioning (see Table 15.5). Read across rows for probabilities of movement between strata (e.g., daily probability of moving from NE to SE was 0.438).

Stratum	Stratum			
	NE	NW	SE	SW
NE	–	0.047 (0.012–0.169)	0.438 (0.297–0.590)	0.058 (0.014–0.204)
NW	0.101 (0.042–0.225)	–	0.308 (0.195–0.450)	0.068 (0.023–0.186)
SE	0.005 (0.001–0.036)	0.030 (0.014–0.063)	–	0.219 (0.169–0.279)
SW	0.022 (0.004–0.102)	0.092 (0.052–0.157)	0.255 (0.165–0.371)	–

Table 15.5.

Results from Program MARK for multi-strata modeling of roost-switching by lactating female big brown bats within HF building, Fort Collins, Colorado. For each model we list the model name (p is capture probability and ψ is transition probability), the Akaike Information Criterion corrected for overdispersion ($QAIC_c$), the $\Delta QAIC_c$, $QAIC_c$ weight, and number of parameters (K). Overdispersion (\hat{c}) was estimated to be 2.5. Strata were NE, NW, SE, and SW locations of building. Apparent survival (ϕ) was assumed to be constant for all models.

Model	$\Delta QAIC_c$	$QAIC_c$	$QAIC_c$ Weight	K
{ p All (.), ψ All (Δt)} ^{a,b}	481.49	0.00	0.38	21
{ p All (.), ψ All (.)}	481.60	0.11	0.36	20
{ p All (.), ψ All (Steat)} ^c	483.70	2.21	0.13	21
{ p All (.), ψ All (Steat + Δt)}	483.71	2.22	0.13	22
{ p All (time), ψ All (.)}	521.48	39.99	0.00	68
{ p All (time), ψ All (Δt)}	523.00	41.51	0.00	69
{ p All (time), ψ All (Steat)}	523.72	42.23	0.00	69
{ p All (time), ψ All (Steat + Δt)}	525.30	43.81	0.00	70
{ p All (.), ψ All (time)}	839.14	357.66	0.00	164
{ p All (time), ψ All (time)}	1086.25	604.77	0.00	212

^a "All" in model name means each of the four strata were modeled the same.

^b Δt is high temperature minus low temperature the day before transition.

^c Steat is the count of individual mites (*Steatonyssus* sp.) on each bat.

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between SE and SW roosting sites also were generally higher than those between NE and NW (Table 15.4). These changes may have reflected the differential exposure of the roosts to the sun on north and south sides and a preference of bats to be on warmer south-facing sides as lactation progresses.

The best model in our example (Table 15.5) included constant capture probabilities and an effect of Δt on the transition probabilities. That is, probability of movement of bats varied on a daily basis and co-varied with the scope of temperature change the previous day. Based on the top four models, our results also showed some support for the hypothesis that the number of ectoparasites may have influenced whether a bat moved to another roost site. Models incorporating a time effect on the transition probabilities were less parsimonious than models incorporating the individual covariate (ectoparasites) and the environmental variable (Δt). Future applications in our study will include larger samples of bats and roosts and will consider additional biological hypotheses, locations, time frames, and alternative covariates (e.g., direct temperature measurements within roosts, counts of other ectoparasites) that may better represent the hypotheses under consideration. Although results from this example should be considered preliminary, they illustrate the potential uses of combining new marking approaches in a more rigorous analytical framework than those previously used in most studies of bat survival and movements.

Conclusions

Most studies of survival in bats used ad hoc procedures for estimation of survival rates. However, recent innovations in modeling of survival using maximum-likelihood-based analytical methods and new software applications provide better opportunities to obtain more reliable estimates. A few recent studies of bats have taken such a probabilistic approach to survival estimation (e.g., Baker et al. 2001; Boyd and Stebbings 1989; Hoyle et al. 2001; Sendor and Simon 2003). Future researchers should follow these recent examples, rather than repeat the ad hoc intuitive regression, life table, and other approaches more widely used in the past. Additionally, most previous studies of survival in bats had drawbacks in that methods of marking and recapturing individual bats had the potential to cause injury, decrease survival, or involved other possible biases. We recommend that alternative marking methods continue to be explored for studies of survival in bats. Recent case examples combining an alternative marking technology (PIT tags) with modern analytical approaches from our own work

suggest that advances in estimating survival in bats are indeed feasible. We also recommend that future research on survival and transition rates in bats strive to construct biological hypotheses about these critical traits and that hypotheses be evaluated using freely available modern software such as Program MARK (available at <http://www.cnr.colostate.edu/~gwhite/mark/mark.htm>) and its embedded model selection procedures that are particularly well suited to the study of these probabilities.

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Appendix 15.1.

Summary of studies of survival rates in bats See Mohr (1952) for summaries of studies reporting recapture rates before 1950. Abbreviations:

A= adult, AF = adult female; AIC = Akaike's Information Criteria;
 AM = adult male; BM = Bezem method; CJS = Cormack-Jolly-Seber;
 F = female; GLG = growth layer groups in tooth sections;
 GOF = goodness-of-fit; IR = intuitive regression approach; J = juvenile;
 KAC = known-age cohorts; LT = life table; M = male; SC = survivorship
 curve; SE = standard error; subA = subadult; UAC = unaged cohorts.

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
<i>Antrozous pallidus</i> , <i>Eptesicus fuscus</i> , Arizona, 1980-1995	Bands, 1,702 <i>A. pallidus</i> , 2,231 <i>E. fuscus</i> , 2 nurseries each; LT from KAC.	Descriptive; age, species contrasts; correspondence with environmental factors.	1st-year F survival lowest (means 0.42-0.49 <i>A. pallidus</i> , 0.53-0.64 <i>E. fuscus</i>). Annual mean AF survival 0.29-0.76 <i>A. pallidus</i> , 0.71-0.90 <i>E. fuscus</i> .	Sidner (1997)
<i>Artibeus jamaicensis</i> , Panama, 1976-1980	Bead necklaces, mist-netting forest roosts; 8,907. % recap or % known alive by half-year intervals, some KAC (J, subA, A). Sexes, ages, marking periods treated separately. Chi-square tests on % recap among groups. Leigh and Handley (1991) assumed constant, identical survival process as an earlier study; implies no individual heterogeneity in survival and capture probabilities; also used IR.	Descriptive; differential survival sexes, age classes, birth season of J.	J survival < A, J born spring > J born autumn. Suggested AF survival > AM. Tag loss. Leigh and Handley (1991) calculated annual survival of 0.58. Survival appears low, but survival and capture probabilities confounded.	Gardner et al. (1991); Leigh and Handley (1991)

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
<i>Balionopteryx plicata</i> , <i>Rhynchonycteris naso</i> , <i>Saccopteryx bilineata</i> , <i>S. leptura</i> , Costa Rica, 1973	Ad hoc surrogate, females only, (% of females captured with used teats, parturition rates) <i>n</i> unspecified.	Descriptive, differ- ences based on habitat stability.	<i>B. plicata</i> 54%, <i>R. naso</i> >78%, <i>S. bilineata</i> 78%, <i>S. leptura</i> >78%.	Bradbury and Vehrencamp (1976, 1977)
<i>Carollia perspicillata</i> , Costa Rica, 1974–1984	Bands, beaded neck- laces, 3,253, UAC IR/LT approach; annual changes in tooth wear classes; % in cave recap- tured after 1 yr.	Descriptive; differ- ential survival of AF, AM, J.	Young recap < A; young F recap < young M (likely differential disper- sal); AM, AF similar % recap. Tag loss.	Fleming (1988)
<i>Chalinolobus</i> <i>morio</i> , <i>Nyctophilus</i> <i>geoffroyi</i> , <i>Vespadelus</i> <i>vulturinus</i> , Australia, years unspecified	Bands, 10–12 yr periods, 1,870– 3,936 (varied with species), colony type unspecified; CJS estimate ϕ Program JOLLY, time-varying p_i and ϕ .	Band type, degree of injury affected ϕ . Differences in ϕ by band type within species tested by Behrens- Fisher t-tests.	Differences by band type in <i>N.</i> <i>geoffroyi</i> ($0.19 \pm$ 0.05 SE Monel bat bands, 0.42 ± 0.12 Mg-Al bird bands). Age, sex unspecified. Highest annual ϕ for <i>V. vulturinus</i> 0.59 ± 0.10 ; <i>C.</i> <i>morio</i> 0.72 ± 0.04 .	Baker et al. (2001)
<i>Corynorhinus</i> <i>townsendii</i> , California, 1947–1951	Bands, AF, J, 2 nurseries, 85 and 60 AF, also hiber- nacula. % recap- tured.	Descriptive	40–54 % J return after 1 yr; 70–80% AF return annually.	Pearson et al. (1952)
<i>Desmodus rotundus</i> , Mexico and Argentina, 1969	GLG teeth, 217, sexes combined. SC (age vs. % in sample). GLG not validated with known-age specimens.	Descriptive	SC. Assumed con- stant reproduction, stationary age dis- tribution.	Lord et al. (1976)
<i>Desmodus rotundus</i> , Argentina and Brazil, years unspecified	GLG teeth, 87, sexes combined. SC (number GLG vs. number of bats). GLG not validated with known-age specimens.	Descriptive	SC	Linhart (1973)
<i>Eptesicus fuscus</i> , Minnesota, 1940– 1954	Bands, 3,871, hiber- nacula; UAC, in- correct ad hoc band recovery methods.	Descriptive	“over-all mortality rate of about 40 per- cent per year” (Beer 1955:245); survival lowest 1st yr.	Beer (1955)

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
<i>Eptesicus fuscus</i> , Minnesota, ca. 1951–1971	Bands, 960, hibernaculum; UAC, % alive vs. yrs after banding by sex.	Descriptive	Survival 60% 1st yr after banding, higher thereafter.	Goehring (1972)
<i>Eptesicus fuscus</i> , Minnesota, ca. 1951–1971	Bands, IR	Descriptive	Annual survival AM 0.82, AF 0.74.	Hitchcock et al. (1984), based on Goehring (1972)
<i>Eptesicus fuscus</i> , Ohio, 1969–1972	Bands, 110 and 142, 2 nurseries, KAC, IR/LT at 1–3 yrs after banding.	Descriptive	% recap colony 1, colony 2: yr 1 32%, 10%; yr 2 71%, 70%; yr 3 28%, 57%. Declines (88% and 60%) thought due to study.	Mills et al. (1975)
<i>Eptesicus fuscus</i> , Ohio and Penn- sylvania, 1965–1967	Bands, ~39–72, 2 nurseries (Ohio, Pennsylvania); % of F recaptured after 1 yr.	Descriptive	Ohio: AF return 53% in 1966, 24% 1967; J 32% 1966, 17% 1967. Penn: AF 21% 1966, 10% 1967; J 14% 1966, 12% 1967.	Brenner (1968)
<i>Macroderma gigas</i> , Queensland Australia, 1976–1980	Ear tags, 268, mist nets, caves. Tropical. Recaps in 3-mo seasons. CJS model in MARK, GOF tests RELEASE; used MARK to test for trap dependency, bootstrap estimate overdispersion parameter. A treated separately from an age-structured model based on 163 bats first caught as J.	AIC model selec- tion for A ϕ . Sex, time, season, year, rainfall (flooding roosts), tempera- ture as group factors or covar- iates.	Best model for A ϕ included sex, season, rainfall. AF annual ϕ (0.57–0.77) > AM (0.43–0.66). AIC support for rain- fall, sex, tempera- ture effects for J. 1st yr ϕ JF 0.35– 0.46, JM 0.29–0.42. Tag loss.	Hoyle et al. (2001)
<i>Miniopterus schreibersi</i> , NSW Australia, 1960–1963	Bands, toe clips, 8,775, nurseries and nonbreeding sites; estimated % as yearlings, adults, arithmetically com- puted survival that would yield this age distribution.	Descriptive	A survival ~0.75.	Dwyer (1966)

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
<i>Miniopterus schreibersi</i> , <i>Myotis macrodactylus</i> , <i>Rhinolophus ferrum-equinum</i> , Japan, ca. 1966-1980	Bands, 2,795 <i>M. schreibersi</i> , 1,924 <i>M. macrodactylus</i> , 3,707 <i>R. ferrum-equinum</i> ; nursery, hibernacula; % recaptured 1-14 yrs after banding.	Descriptive	AF % recaptured > AM in <i>M. schreibersi</i> , sexes similar in <i>Myotis</i> .	Kuramoto et al. (1985)
<i>Myotis austroriparius</i> , Florida, 1952-1955	Bands, 1,998, nurseries; % recap by age at 1, 2 or \geq 3 yrs.	Descriptive	Recap ~47% yr 1, 18% yr 2, 35 % \geq yr 3.	Rice (1957)
<i>Myotis dasycneme</i> , Netherlands, 1955-1962	Bands, 179 AF, nursery; BM.	Descriptive; compared estimates at winter vs. summer banding sites.	Annual AF survival similar summer (0.70) and winter (0.67) colonies; > % injury bats banded summer.	Sluiter et al. (1971)
<i>Myotis dasycneme</i> , 1940-57; <i>M. daubentoni</i> , 1945-1957; <i>M. emarginatus</i> , 1945-1955; <i>M. myotis</i> , 1940-1955; <i>M. mystacinus</i> , 1945-1957; <i>Rhinolophus hipposideros</i> , 1942-1956; Netherlands	Bands, hibernacula 1,191 <i>M. dasycneme</i> ; 920 <i>M. daubentoni</i> ; 1,608 <i>M. emarginatus</i> ; 650 <i>M. myotis</i> ; 1,828 <i>M. mystacinus</i> ; 1,717 <i>R. hipposideros</i> . BM.	Descriptive; differences by 1 cave groups in 3 species <i>Myotis</i> , sex in all (ANOVA on slopes and intercepts).	AF, AM survival similar all species; F = M capture rates in all, except <i>M. daubentoni</i> . No diffs in survival but diffs in capture rates between caves for 3 species. Annual survival for 5 species of <i>Myotis</i> range 0.64-0.80, 0.57 in <i>R. hipposideros</i> .	Bezem et al. (1960)
<i>Myotis grisescens</i> , Missouri, 1968-1978	Bands, 18,632 banded 2 yrs, 1 hibernaculum, UAC; IR by sex.	Descriptive	M annual survival 70%, F 73%; lower rates 1st yr.	Elder and Gunier (1981)
<i>Myotis grisescens</i> , Alabama, Tennessee, ca. 1968-1976	Bands, ca. 3,946 at 3 nurseries, recap at 2 hibernacula. J, yearling and A cohorts. IR/LT; non-parametric trend tests on % recap.	Differential survival at declining and stable maternity colonies, sex and age class diffs.	Survival similar by sex, age. 1st yr estimates very variable, 0.06-0.73; 0.57-0.85 thereafter. Survival reflects changes in counts.	Stevenson and Tuttle (1981)

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
<i>Myotis leibii</i> , Ontario, 1941–1948	Bands, 258, hibernaculum, CJS model.	Differential survival of sexes.	AM ϕ 0.76 ± 0.11 SE (range 0.60–0.89, 5 estimates). AF ϕ 0.42 ± 0.07 (range 0.17–1.0, 5 estimates). $P = 0.01$, z-test.	Hitchcock et al. (1984)
<i>Myotis lucifugus</i> , Ontario, ca. 1947–1962	Bands, 1,936 bats at 1 hibernaculum; CJS model, tested rates using z-test; compared results BM, IR/LT.	Differences by sex.	Annual survival of AM (0.82 ± 0.01) > AF (0.71 ± 0.02).	Keen and Hitchcock (1980)
<i>Myotis lucifugus</i> , Indiana and Kentucky 1953–1969	Bands, > 24,000; 386 cohorts from multiple nurseries, 278 cohorts from multiple hibernacula; IR/LT, estimates across multiple colonies, cohorts from nurseries defined as adult or immature at banding, UAC at hibernacula.	Descriptive	Not all roosts sampled annually, selected subsets with highest numbers alive as typical for semi-log plots. Survival 1st yr after banding (13–49%) < subsequent yrs (54–86%).	Humphrey and Cope (1976)
<i>Myotis lucifugus</i> , Pennsylvania, ca. 1965–1969	Bands, 2,914, hibernaculum; number recap annually, LT.	Descriptive	1st yr survival lowest.	Brenner (1974)
<i>Myotis lucifugus</i> , Alberta, ca. 1975	GLG, 90 AF collected at maternity colony, SC from % each age class.	Descriptive		Schowalter et al. (1978)
<i>Myotis myotis</i> , Germany, 1991–1994	Bands, 232 JF at 4 nurseries, reappearance rates 1 yr later; J carcasses as % of J present.	Descriptive	F reappearance after 1st winter varied by yr and colony (0–40%).	Zahn (1999)
<i>Myotis mystacinus</i> , Netherlands, 1942–1956	Bands, n not clearly specified; hibernacula, BM.	Descriptive, differences by cave, sex.	AM, AF survival similar at 0.79.	Sluiter et al. (1956)

Species, Location, Years	Methods and Sample	Hypotheses Tested	Summary of Findings, Comments	Reference
<i>Myotis sodalis</i> , Indiana, ca. 1956– 1973	Bands, 4 M and 3 F cohorts at 2 hibernacula; UAC, IR/LT.	Descriptive	AM, AF SC similar. Lowest survival 1st yr after marking, last few yrs. A survival highest and constant at yrs 1–6 (F 0.76, M 0.70), lower and constant at yrs 6–10 (F 0.66, M 0.36).	Humphrey and Cope (1977)
<i>Nycticeus humeralis</i> , Indiana, 1958–1964	Bands, 526, 2 nur- series, % recap for UAC, J, A, 1–4 yrs after banding.	Descriptive	1st yr % recap 0.23–0.32; AF ca. 0.60.	Humphrey and Cope (1970)
<i>Pipistrellus abramus</i> , Japan, 1971–1975	Bands, 315 in 2 nur- series; SC, % known alive, LT; GLG in killed sample of 106 at 1 colony.	Descriptive	“Disappearance rates” (Funakoshi and Uchida 1982: 60) of F to 1 yr 0.18–0.29, 0.39 in 2nd yr; M 0.85– 0.96 in 1st yr. Based on LT of GLG classes, sur- vival in bats age 3–5 < bats age 1–2.	Funakoshi and Uchida (1982)
<i>Pipistrellus pipistrellus</i> , Sweden, 1981–1988	Bands, 1,253, bat boxes in summer, CJS model.	Differential sur- vival of sexes due to male territori- ality; seasonal climatic influences on annual varia- tion.	Annual survival AM = 0.44 (ranges of variances 0.010– 0.026), AF = 0.54 (0.005–0.097). $P <$ 0.05, likelihood test.	Gerell and Lundberg (1990)
<i>Pipistrellus pipistrellus</i> , England, 1977–1984	Bands, 90 AF 55 JF, 2 nurseries; UAC, IR/LT.	Descriptive	Annual survival AF = 0.64, seem- ingly constant. J survival lower 1st yr.	Thompson (1987)

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<i>Pipistrellus pipistrellus</i> , Germany, 1996–2000	Bands, 4,857 AF, 3,263 AM, 4,408 JF, 3,311 JM; one site used as both hibernaculum and “swarming” at night in summer; bats only caught while in flight to minimize disturbance; CJS models following Lebreton et al. (1992), program MARK, AIC _c .	Modeled effects of sex, age, time, season, winter severity on survival, and effort on capture probabilities.	Survival varied by age class and was time-dependent; no effects by sex, and survival was not lower in winter. Annual survival A = 0.80 (SE 0.05), J = 0.53 (SE 0.10). Transience effects noted.	Sendor and Simon (2003)
<i>Pipistrellus subflavus</i> , West Virginia, 1952–1965	Bands, 2 hibernacula, IR/LT each sex. Ad hoc correction to % recaptured using number alive but not recaptured. Justification for the form of the correction not provided, properties unknown.	Descriptive. Age independence of survival.	Survival age-dependent: low yrs 1, 2 (0.41, 0.51 F, 0.46, 0.68 M), increased to yrs 3–4 (0.74, 0.51 AF, 0.98, 0.81 AM), declined to yrs 10–14.	Davis (1966b)
<i>Plecotus auritus</i> , <i>P. austriacus</i> , England, ca. 1960–1969	Bands, year-round colony, 16–20 <i>P. auritus</i> , 5–15 <i>P. austriacus</i> known alive each yr; IR/LT.	Descriptive	Annual survival AM <i>P. auritus</i> 0.54, AF 0.76, <i>P. austriacus</i> AM 0.45, AF 0.62.	Stebbings (1966, 1970)
<i>Plecotus auritus</i> , England, 1975–1985	Bands, 401, nurseries in bat boxes. Two methods: KAC IR, CJS.	Descriptive; comparisons of analytical methods. Integrated with reproduction, sex ratio, and population size information.	Geometric mean annual survival estimates 0.78 ± 0.03 SE AF (range 0.68–0.98 over 9 annual estimates), 0.62 ± 0.08 SE AM (range 0.49–0.94). AF survival = 0.86 using regression corrected for rate of increase and age skewness; uncorrected estimate AF = 0.80, AM = 0.60.	Boyd and Stebbings (1989)

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<i>Rhinolophus ferrumequinum</i> , England, 1948-1958	Bands, 1,808, primarily hibernacula. Number known alive each yr after banding.	Descriptive	Simple reporting of number banded and number known alive by yr.	Hooper (1983)
<i>Rhinolophus ferrumequinum</i> , England, ca. 1970-1986	Bands, toe claw clipping J, hibernacula and nurseries, hand captures. IR/LT, UAC and KAC separately.	Descriptive: AM vs. AF, J vs. A, survival, survival by season.	M, F SC similar. Survival to ages 1 (0.65) and 2 (0.62) lowest. Annual survival increases to 0.86 at age 9. Survival lowest winter, % varied by yr from 0.55 to 0.85.	Stebbing and Arnold (1987)
<i>Tadarida brasiliensis</i> , Texas, 1957-1958	Ad hoc extrapolation from relative areas of hypothetical SCs, and best fit by age ratios based on 3 classes of tooth wear in 22,498 Fs.	Descriptive	AF survival of 70-80% "reasonable" (Davis et al. 1962: 337) based on age class ratios.	Davis et al. (1962)
<i>Taphozous georgianus</i> , Australia, 1985-1989	Bands, 229 J, mist nets at caves, subtropical. IR/LT.	Descriptive	Annual survival F 0.42-0.75, M 0.24-0.66.	Jolly (1990)