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**STUDIES OF BATS IN SOUTHEASTERN ARIZONA  
WITH EMPHASIS ON ASPECTS OF LIFE HISTORY  
OF *ANTROZOUS PALLIDUS* AND *EPTESICUS FUSCUS***

by

**Rhonda Marie Sidner**

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**A Dissertation Submitted to the Faculty of the  
DEPARTMENT OF ECOLOGY AND EVOLUTIONARY BIOLOGY**

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For the Degree of**

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As members of the Final Examination Committee, we certify that we have read the dissertation prepared by Rhonda Marie Sidner

entitled Studies of Bats in Southeastern Arizona With Emphasis

on Aspects of Life History of

Antrozous pallidus and Eptesicus fuscus

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## ABSTRACT

During 1980-1995, 42 cohorts of free-living juvenile female *Antrozous pallidus* and *Eptesicus fuscus* were banded and recaptured at three bridge roosts in Chihuahuan desertscrub in southeastern Arizona. Surviving female colony members returned each Spring to rear young. Life tables from known-age cohorts provided comparison of survivorship within and between populations sharing similar macro-environmental conditions at these maternity roosts.

Mean first-year survivorship varied between and within species and roosts and was higher for *E. fuscus* than for *A. pallidus*. First-year survivorship was affected by weather, by age of mothers through indirect influence on neonate size with number of young in the litter, and by human activity. Disease, predation, inclement weather, and human vandalism caused mortality. Second and third-year survivorship was higher than juvenile year for both species. *Eptesicus fuscus* had higher adult survivorship than *A. pallidus*.

Compared to *A. pallidus*, female *E. fuscus* had lower mortality rates, and females decreased their reproductive effort by litter size reduction and deferred age of first reproduction. While *A. pallidus* females began reproducing at yearling age, 54% of *E. fuscus* females deferred their first reproduction until age two. Fifty-five percent of age two *A. pallidus* and up to 100% of older females produced twins. By contrast, only 9% of age two *E. fuscus* had twins, and < 28% of older females produced

twins. Lower annual productivity by *E. fuscus* females was apparently balanced by longer life. While no more than 10% of *A. pallidus* reached five years of age, at least 10% of *E. fuscus* attained eight years. Thus, these species have evolved a life history that allows reproductive replacement with low fecundity and high survivorship.

Western populations of *E. f. pallidus* produced smaller litters, deferred first reproduction, and had higher juvenile and adult survivorship than reported for *E. f. fuscus*, demonstrating intraspecific geographical differences in life history.

Maximum life-span records for *A. pallidus* were a 10-year old male and a female that was at least 11 years old. The oldest *E. fuscus* were two females that were at least 14 and 15 years old.

#### 4. INTRODUCTION

Of approximately 4060 recognized species of mammals, 853 of these (21%) are members of the Order Chiroptera (Vaughan, 1986). While all bats share the ability to fly, and in consequence possess the corresponding physiological, morphological, and reproductive traits that are required by this ability, there is also remarkable variability within this group of flying mammals. This great diversity and richness of species makes these animals of unusual importance as subjects of various ecological studies that involve not only comparisons with other members of this Order, but with other orders of mammals, and non-mammals as well.

One of the basic concerns of ecology is the detection and analysis of the patterns and processes of variation in life history (Boyce, 1988). The observed continuum of breeding strategies ranges from species who breed once with tremendous output in their unique effort to those that breed repeatedly over considerable time (Pianka, 1978). Most species of mammals are found along the latter end of this continuum in a zone of iteroparous breeding, and differences in their breeding patterns have to do with the size of their repeated litters and the scale of time within which these litters occur, although there are exceptions (Braithwaite and Lee, 1979).

Bats are an intriguing group for life history study, because they are an oddity in the mammalian paradigm of physiological and ecological characteristics that scale

with body size. As small mammals, bats are notable because of their long life span, reduced number of litters per year, long gestation period, small litter size, slow development to sexual maturity, large home range, and low adult mortality (McKean and Hamilton-Smith, 1967; McNab, 1982). And yet, even though bats comprise the second largest order of mammals, there have been few studies that report consequences to life history of these notably unusual traits. These characteristics suggest that bats live in stable, predictable types of environments where selection tends to promote small litter size and strong parental care of young (Findley, 1993).

These physiological and ecological characteristics that differ from predictions for their body size, affect their life histories. Because of their small body size and the associated problem of relatively large surface area to volume ratio—which is made more extreme by the increased surface area of the skin wings that provide the benefits of flight—bats in temperate zones have evolved adaptations for conserving body heat and moisture. For this reason, roosts are of supreme importance to bats, in part because the roost provides thermal benefits allowing suitable heterothermic adjustment, and because roosts provide critical protection from predators, especially when bats are most susceptible, in a lethargic—but energy conservative—state of torpor (Humphrey and Cope, 1976).

When resources are limited, models of energy allocation predict selection for large litter size and rapid juvenile growth during the auspicious growing season,

because abundant food should enhance juvenile growth and survival, and adult fitness would increase as a result (Boyce, 1988). In the temperate zone, including the deserts of North America, where animals face the problem of seasonality, the production of young must take place during a short season with favorable climatic conditions and abundant food resources that are appropriate to fuel pregnancy, lactation, recovery by postparturient females, and growth of potentially many young. For bats, which are constrained to produce a limited number of altricial young because of the aerodynamic burden of carrying fetal weight, the short season may be even more problematic. Postnatal growth of altricial young must be rapid not only to allow attainment of adult size and body fat reserves before the unfavorable season (Ransome, 1995), but also to allow time to develop the intricacies of foraging in the air at night.

Allocation theory also predicts, however, that if the abundance of food also causes adult survival to increase, selection should endorse reduced reproductive effort and increased allocation to adult body maintenance (Boyce, 1988), because higher expectation of survival translates into future reproduction.

It has been suggested that birds and bats, because of flight, enjoy higher survivorship, because they have been released from the kind of predation that usually causes high mortality in small animals. In addition, roosting in caves may make bats even less susceptible than birds to mortality factors, because of the protection

afforded by the roost (Humphrey, 1975). Again, the prediction is that under such conditions, bats should respond to increased survivorship by producing smaller litters. A comparison within the vespertilionids supports the contention that bats that enjoy higher survivorship produce smaller litters; the majority of species of cave-roosting bats in North America have litter sizes of one young, while most foliage-roosting bats (i.e., the species of *Lasiurus* and *Lasiomycteris*) that use relatively less protected sites, have two to four young per litter (Cockrum, 1955). If adult bats do enjoy thermal benefits and protection through the use of certain types of roosts, and in consequence reduce their reproductive effort, then allocation of body energy to maintenance functions such as fat accumulation would result in higher survivorship during winter. The temporary decrease in productivity due to smaller litter size could be made up in future reproductive events, especially since adult bats have potentially long life span.

A comprehensive review of the literature on bats was published by Kunz (1982) to stimulate research in areas that needed study. One subject for which there is almost no information is the age-specific analysis of life history traits. Life tables have been prepared for several species, but animals of unknown age were the subjects (Tuttle and Stevenson, 1982). A few life tables prepared from known-age cohorts of bats have been published for a handful of species (Table 4-1). Three of these studies were for *E. fuscus* from the eastern U.S., but the studies lasted no more than three years of the long life span of this species.

Table 4-1. Studies reporting age-specific survivorship for bats from known-age cohorts of juveniles (Tuttle and Stevenson, 1982). Survivorship is expressed as percent of banded animals that survived to the next year.

Species	Length of Study	Juvenile Females	Adult Females	Reference
<i>E. fuscus</i> (East)	10 months	34.8%	60.5% (unknown age)	Davis, 1967
<i>E. fuscus</i> (East)	3 years	~15-30% estimated from graph	~20-50% estimated from graph	Brenner, 1968
<i>E. fuscus</i> (East): cohort A	3 years	Year 1: 31.9%	Year 2: 71.3% Year 3: 28.0%	Mills et al., 1975
<i>E. fuscus</i> (East): cohort B	3 years	Year 1: 10.5%	Year 2: 70.0% Year 3: 57.1%	Mills et al., 1975
<i>Nycticeius humeralis</i>	1 year	Year 1: 23-32%	Year 2: 60%	Humphrey and Cope, 1976
<i>Plecotus townsendii</i>	3 years	Year 1: 38-54% at three sites	Year 2: 75% Year 3: 80%	Pearson et al., 1952
<i>Myotis grisescens</i>	1 year	13.9-58.6%	---	Stevenson and Tuttle, 1981

Other individual components of life history have been described for some species of bats. For example, data are available for maximum recorded longevity (Tuttle and Stevenson, 1982), litter size (Cockrum, 1955), and age of first reproduction (Tuttle and Stevenson, 1982), but much of this information for bats is sketchy, outdated, or scattered throughout somewhat unavailable literature. When Cockrum (1973) published an impressive list of longevity records for 16 species of bats in Arizona, it appeared that *A. pallidus* and *E. fuscus* shared similar life spans of 9 to 10 years. A new record of 20 years was reported for *E. fuscus* (Davis, 1986), but nothing new has been contributed for *A. pallidus*. There is a need for this kind of data. For example, when McNab (1982) discussed the energetics of bats and life span, he described a "low" life-span ratio without numbers for *A. pallidus*, because he required more information on pallid bat longevity before he could quantify the ratio.

In some studies, a particular life history trait, for example, litter size, has been compared to the general age of bats, i.e., juvenile versus adult classification (R. Davis, 1969b). However, there are notably few studies published with age-specific analyses of these and other life history parameters. The age-specific aspect of most reproductive and survival parameters is a critical part of the life history package that defines a species. Charlesworth (1994) explains that traditionally, all species were treated as having fecundities and survival rates that were independent of age, when,

in fact, many species are actually age-structured; only recently have genetic and ecological theories been modified to include this age-structure. He notes a recent increase in empirical tests of life-history since the addition of age-structured population analysis. But such analysis has not been evident in the bat literature. Only recently, has a study of the details of life history features been compared to the specific age of mothers (Ransome and McOwat, 1994). In consequence, there are many unanswered questions. Do different individuals in a population vary their litter size or postpone reproduction altogether; if so, why? Is offspring survivorship within a species correlated with the age of the mother?

The life history characteristics that we observe are a result of natural selection acting on individual variation in a population to increase lifetime reproductive success for a species in its particular environment. Differences in life history within and between species beg comparison. Within certain families of bats, such as the vespertilionids, some species have broad geographic distribution, and provide the opportunity to make comparisons of life history strategies on a biogeographical basis, not only between species, but within species from different regions with potentially different environmental factors. Why do populations of a species in one region have a different litter size than populations of conspecifics in a different geographical region? Do similar species that live together in the same environment and potentially face the same influences on mortality share the same strategy for number of offspring

produced? Are mortality rates higher within one population than another? Almost no such comparative studies have been made for bats (Tuttle and Stevenson, 1982).

Interspecific comparisons of life history variation are valuable (Boyce, 1988; Eisenberg, 1981) for revealing patterns that otherwise might not be apparent. Similar characteristics between different species suggest convergent evolution in response to the same selective forces, while the source of similar characteristics within populations of the same species may not be discernible and may just be due to phylogeny. Thus, cross-taxonomic study may be necessary to reveal patterns of life history variation (Harvey and Read, 1988).

Few studies of bats, however, provide data to make possible the comparison of survival between and among species in response to different environments; and as a result, the survival strategies of bats are not well known (Tuttle and Stevenson, 1982). There have been studies of survivorship for a few species, such as the well-known long-term record of population ecology of *Myotis lucifugus* (Humphrey and Cope, 1976), but many of these earlier works actually report return rates rather than survival rates of bat populations. This is because survivorship studies typically were conducted on mixed cohorts of bats of unknown age, principally because the bats were first banded at winter hibernacula where precise aging is nearly impossible (Humphrey and Cope, 1976; Tuttle and Stevenson, 1982). While these studies have provided much information about bats, they contain the pitfalls of using un-aged

cohort analysis, or sampling marked animals from huge numbers of bats in a roost. These problems have been reviewed (Caughley, 1977; Keen, 1988; Ransome, 1995; Tuttle and Stevenson, 1982 ). For example, one of the problems of using a sample of animals in a cohort rather than using the complete cohort in a survivorship study is that the analysis of estimates of annual survival rates assumes that survival is independent of age, but it is well-documented that this assumption is incorrect for most mammals (Caughley, 1977) and for at least a few species of bats (Ransome, 1995).

Many causes of mortality to bats have been described, and these include such things as human disturbance (both intentional and unintentional types) whether it be direct or indirect (e.g., through direct application of poisons such as pesticides or through indirect loss of habitat as from urban development), predators of many kinds and other biological agents such as ectoparasites and disease organisms, and they include harsh weather conditions, and even phase of the moon. Other factors intrinsic to the organism affect, in particular, the survivorship of young bats. These factors include, for example, the age and condition of mothers, the timing and synchrony of birth, the size of the colony into which the bat is born, the litter size, the size and stage of development of young at birth, and possibly even its sex (Tuttle and Stevenson, 1982).

Most of the reported causes of death to bats have been described without quantifying their influence on survivorship rates. In particular, age-specific mortality has not been determined for many species of bats.

In southeastern Arizona, as a result of both low latitude and considerable variability in elevation and topography, there is relatively high species richness of small mammals (Lomolino et al., 1989), and especially in the mammalian Order Chiroptera (Wilson, 1974). In fact, within Arizona, south of the Mogollon Rim, and east of the Baboquivari Mountains, 25 species of bats are known to occur as either year-around residents or seasonal visitors (Hoffmeister, 1986; Sidner and R. Davis, 1995). In part, this richness of bats is due to the diversity of available types of roosts associated with the diversity of habitat (Humphrey, 1975). The habitats occupied by these species range from the deserts at the lower elevations to conifer forests at the higher elevations on the isolated mountains, and some of the individual species occur throughout all those habitats. These chiropteran species are potential subjects for comparative investigations of the ecological processes that select for different life history strategies in different environments. Two of these species that are widespread, common, and abundant throughout the entire state in many biotic communities (Hoffmeister, 1986) are the subjects of this dissertation.

#### 4.1 The Species

In the Chihuahuan Desert of southeastern Arizona near Tombstone, populations of two species of bats, *Antrozous pallidus* (the pallid bat) and *Eptesicus fuscus* (the big brown bat), use manmade structures, as maternity roost sites from May to October each year (R. Davis, 1966; Sidner, 1982). Colonies of these bats using the same maternity roost sites, i.e., the expansion joints of the same concrete bridges (R. Davis and Cockrum, 1963), undoubtedly experience micro-environmental differences within each crevice, because the species segregate themselves within the expansion joints, using different ends of the joints and sometimes using different ends of the bridge. But the two species are exposed to the same macro-environmental conditions external to the crevices. Because they face these same conditions on a daily basis and appear to remain relatively stable in population size, they make possible a comparison of their differential responses to the factors affecting survivorship, and in turn, their reproductive output.

Sharing features of the Family Vespertilionidae, *A. pallidus* and *E. fuscus* differ in characteristics such as pelage color, body size, range of distribution, ecological tolerances, and specific feeding habits. Thick and silky, brown fur is characteristic of *E. fuscus*, with dark brown or near-black flight membranes, and short, medium-length ears. In contrast, *A. pallidus* has large ears, large eyes, light-

colored flight membranes, and short, soft fur that is white on the venter, and blonde to light brown on the dorsum.

The two species have nearly identical total body length, but *A. pallidus* has a larger forearm, 45-60 mm, as compared to 39-54 mm for *E. fuscus* (Kurta and Baker, 1990; Hermanson and O'Shea, 1983). In both species there is considerable variation in body mass depending upon the time of year or reproductive state of the female. In consequence, body masses should always be reported with descriptions of season and reproductive status. For *A. pallidus* in southeastern Arizona, mean body mass of females is 17.4 g in the Spring (n = 36), 25.9 g during pregnancy (n = 17), 19.1 g during lactation (n = 76), and 22.2 g (n = 39) in the Fall (R. Davis, 1969a). Mean postpartum body mass of adult female *E. fuscus* is 16.1 g (n = 27) in Massachusetts (Burnett and Kunz, 1982).

The genus *Eptesicus* is worldwide in distribution. In the New World, *E. fuscus* is abundant in Alaska, across all of southern Canada, southward throughout the U.S., Mexico, Central America, the Caribbean Islands, and into northern South America (Hall, 1981). *Antrozous* is a New World endemic genus. The distribution of *A. pallidus* is more limited than *E. fuscus*, in western North America from the southern edge of British Columbia southward, through the west coast states of the U.S. and Baja California, east to Montana (Shryer, 1980), Wyoming (Clark and Stromberg, 1987), Kansas, and west Texas; and continues south through Mexico to

Jalisco and Querétaro. The other species in the genus reach through the base of the Yucatan peninsula from Veracruz to Belize, east to Nicaragua, south to Costa Rica, and east to Cuba (Hall, 1981).

Most abundant in desert habitats of the Lower Sonoran Life Zone in western U.S. and Mexico, *A. pallidus* also occurs in grasslands and pine forests (Hermanson and O'Shea, 1983). During survey work in many of the mountain islands in southeastern Arizona, I have found *A. pallidus* in habitats ranging from Sonoran and Chihuahuan desertscrub, through semidesert grassland, Madrean oak woodlands, and less frequently, in ponderosa pine forest (R. Davis and Sidner, 1992).

While both *A. pallidus* and *E. fuscus* occur together in southeastern Arizona in the same manmade structures, sharing the same conditions during the birth and rearing of their young, they tend to be found predominantly in different habitats; *A. pallidus* in arid habitats, and *E. fuscus* in both arid, but more frequently, in mesic habitats. Only 30% of 97 localities reported by Hoffmeister (1986) for *E. fuscus* were in desertscrub habitats, while 70% were from grassland, wooded, and forest habitats; 49% of 69 localities for *A. pallidus* were in desertscrub (Hoffmeister, 1986). Of 24 species of bats I have observed in southeastern Arizona, *E. fuscus* has been the most ubiquitous, found in each surveyed area in all biotic communities when water was nearby. For example, in samples from Saguaro National Park, *E. fuscus* comprised 38% of 186 bats of 11 species netted over a pond in ponderosa pine forest at 2440 m

elevation, while only one *A. pallidus* was ever observed there (R. Davis and Sidner, 1992).

Adaptations of *A. pallidus* for living in arid environments include the appropriate kidney structure and corresponding ability to concentrate urine much more than most other species of bats in North America that have been tested. Under laboratory conditions (at 25°C and 9.5 mm Hg; mealworm diet) *A. pallidus* can maintain a positive water balance when deprived of free-water for at least one month (Geluso, 1978). The urine concentrating ability of *E. fuscus*, even from desert populations, is poor for conserving water (Geluso, 1978).

During the day, *E. fuscus* roosts in manmade structures like buildings and bridges, and in hollows of trees (including saguaros), in rock crevices (Kurta and Baker, 1990), and I have found them in caves and mine tunnels in which they use crevices or cup-like indentations in the walls. Crevices are preferred by *A. pallidus* during the daytime, including tight spaces in rocky outcroppings and a variety of manmade structures such as buildings and bridges. Contrary to some reports (Hermanson and O'Shea 1983), this species does use crevices in caves and mine tunnels, and in fact, for six years, I have observed a maternity colony of pallid bats using a fissure in a cave-like mine by day, and the inner walls of the mine by night in the transitional oak-grassland habitat of the Huachuca Mountains in southern Arizona. *Antrozous pallidus* produces a conspicuous vocalization, audible to humans, that

reveals their presence in the roost (Orr, 1954). These vocalizations may encourage other bats to rejoin the cluster, a behavior which is beneficial for heat conservation (Trune and Slobodchikoff, 1976).

Both species use relatively exposed surfaces for "night-roosting" purposes, after the initial early-evening foraging trip, and in between other foraging flights, until they eventually return to their more sheltered crevices for day roosting (Hermanson and O'Shea, 1983; Kurta and Baker, 1990). Both species may forage for brief periods throughout the night. *Antrozous pallidus* can be detected by its audible calls as it moves in and out of a night roost at various times. I have heard these vocalizations while they flew outside a mine roost at most hours of the night. Sitting quietly within the roost, with a night vision device, I have watched them returning from a late nocturnal flight to the inner roost where they attached themselves upright against a wall surface and fed upon large arthropods they brought with them.

Both *E. fuscus* and *A. pallidus* prey upon large, hard-bodied arthropods, although they also eat moths (Freeman, 1981; Ross, 1961). There is overlap in diet, but there are no studies of resource partitioning between these two species. In consequence, it is not known whether partitioning might occur when they share the same roost, as has been suggested for conspecific foliage-roosting bats of the genus *Lasiurus*, that partition by species-specific food items but not by hunting times (Hickey et al., 1996). In the current study, *A. pallidus* and *E. fuscus* apparently do

not partition hunting time either, because both species exited the roosts within minutes of each other. The method of foraging is different for *A. pallidus* and *E. fuscus* and may prevent diet overlap when they are sympatric. *Antrozous pallidus* listens passively (without employing echolocation during the approach and attack) to the sounds generated by insect movements and captures prey on the ground (Bell, 1982). Big brown bats, however, capture flying prey while using ultrasonic echolocation and have been studied extensively in research about bat echolocation and the brain (Kurta and Baker, 1990). Further evidence that the two species forage differently comes from analysis of stable carbon isotopes that show that in southern Arizona and other areas where Saguaro cactus and *Agave* plants exist, *A. pallidus* has high levels of body tissue containing carbon ratios that indicate the source of carbon is from plants that employ Crassulacean acid metabolism (Herrera et al, 1993). Presumably, these *A. pallidus* are eating insects that use the cactus and *Agave*. The body tissues of *E. fuscus* in the same area do not contain these same ratios (Herrera et al., 1993).

Many other diagnostic characteristics including physiology, ecology, genetics, echolocation, behavior, and fossil history for these two species are summarized in the Mammalian Species Accounts prepared for each (Hermanson and O'Shea, 1983; Kurta and Baker, 1990).

In southern Arizona the size of young at birth, the age of first reproduction, the developmental stage of young at birth, and the neonatal growth rate have been described for *A. pallidus* (R. Davis, 1969b). These traits are also known for eastern populations of the subspecies, *E. fuscus fuscus* (Burnett and Kunz, 1982; Kunz, 1974). For the western subspecies, *E. f. pallidus*, anecdotes about timing of parturition and litter size are the extent of life history information (Barbour and Davis, 1969) for wild populations. Laboratory newborns of both *A. pallidus* and *E. fuscus* were judged to be altricial because their eyes are closed at birth, and the production of precursor FM echolocation pulses by young bats (Brown and Grinnell, 1980) showed that *A. pallidus* is the most altricial. Wild populations of altricial *A. pallidus* develop more rapidly than laboratory captives (R. Davis, 1969b; Orr, 1954).

Age-dependent litter size production has been reported for *A. pallidus* but not for *E. fuscus*. In southern Arizona, yearling female *A. pallidus* produce one young, and most ( $\geq 66\%$ ) older females produce two young per litter (R. Davis, 1969b). In the western U.S., *E. fuscus* usually is reported to produce one young per litter (Cockrum, 1953; Kunz, 1974), but Schowalter and Gunson (1979) reported from Alberta, Canada that 13% of 115 pregnant *E. fuscus* produced twin young. The apparent higher productivity by eastern *E. fuscus* that produce two young per litter (Burnett and Kunz, 1982) has not been explored.

Studies of homing ability of *A. pallidus* and *E. fuscus* and the growth and development of young, body size, wing loading of pregnant and lactating females and growing juveniles, and age-dependent litter size production by yearling and older adult female *A. pallidus* were conducted at the maternity roosts near Tombstone (R. Davis and Cockrum, 1962a; R. Davis and Cockrum, 1962b; R. Davis, 1966; R. Davis, 1969a; R. Davis, 1969b). In comparison, the reproductive habits and behavior of *E. fuscus* are unknown in Arizona despite the abundance and common occurrence of this species. No maternity colonies had been studied when my investigation began (Hoffmeister, 1986).

In Arizona, since *A. pallidus* generally has two young per year and *E. fuscus* has been thought to have only one young, the two species of bats must deal differently with the potentially competing stresses of survivorship and reproductive output.

No age-specific life tables have been prepared for western populations of *E. fuscus* despite reports of different litter size production between the eastern and western subspecies (Tuttle and Stevenson, 1982). No life tables have been prepared for *A. pallidus* (Hermanson and O'Shea, 1983).

For 15 years, I have studied the age-specific survivorship in these two species that use the same maternity roosts in southern Arizona. In this dissertation, I compare their life histories and emphasize age-specific analysis along with the influence of

maternal age on the survivorship of offspring in order to better understand the factors which contribute to their relative stability and success at these sites. I also compare the life history traits of the western *E. fuscus* with those previously published for eastern populations of the species.

## 5. STUDY AREA AND METHODS

### 5.1 Study Area

I studied five maternity colonies of bats at three roost sites in the Chihuahuan desertscrub biotic community of southeastern Arizona near Tombstone in Cochise Co. (Brown and Lowe, 1983). These roosts are in bridges that are in tributary drainages of the San Pedro River, a major riparian watershed system with seasonally intermittent surface flow. Each site is at a concrete highway bridge over a dry wash. The colonies of *A. pallidus* and *E. fuscus* roost in these bridges in open expansion joints, that run at right angles to the highway (R. Davis and Cockrum, 1963). Bats were known to roost in some of these sites since at least 1959 (R. Davis, 1963) and have continued to occupy these bridges ever since. Two other species of bats (*Tadarida brasiliensis* and *Myotis velifer*) were observed infrequently when they roosted with the primary two species as individuals or in groups of 2-10 bats, but they were always transient animals.

The bridges are surrounded by either private or state lands that are used for cattle grazing; cattle have been observed under the bridges at each roost. Water is available in various types of cattle tanks on these lands. The dry washes and immediate vicinity surrounding them are vegetated by mature mesquites (*Prosopis juliflora*), catclaw (*Acacia greggii*), desert willow (*Chilopsis linearis*), Arizona ash (*Fraxinus velutina*), desert broom (*Baccharis sarothroides*), hackberry tree (*Celtis*

*reticulata*), Arizona walnut (*Juglans major*), whitethorn (*Acacia constricta*), desert sumac (*Rhus microphylla*), tarbush (*Flourensia cernua*), and creosotebush (*Larrea divaricata*) (plant names from Lowe, 1985). The average total annual precipitation for Tombstone (31 deg. 42' and 110 deg. 03') is 324 mm with 224 mm (69%) occurring from May through September (Brown, 1982).

The SD roost is located at 1207 m elevation (USGS, 1958). A colony of *A. pallidus* was first banded there for this study in 1980. In 1982, a few *E. fuscus* were found there, and the following year, and each year after that, a colony of *E. fuscus* was present.

The TM roost is located 8 km southeast of SD, at 1286 m elevation (USGS, 1958). A colony of *E. fuscus* was first banded there for this study in 1981, and each year after the colony became progressively larger. There were no *A. pallidus* at TM.

The TB roost is located 4 km southeast of TM (12 km southeast of SD), at 1304 m elevation (USGS, 1952), next to a trailer park. A colony of *A. pallidus* was first banded there in 1981 for this study, when there were no *E. fuscus* present. In 1982, two adult female big brown bats were present, and during the next four years the *E. fuscus* colony increased in size.

All three roost sites are easily accessible by road, and the bats were relatively easy to capture within the roosts. These features, that facilitated study, also meant that the bats were easily accessible to other humans as well. Occasional flash floods

during the July - September rainy season were sometimes a problem, not only for me, but also for the bats, because water runoff from the road surface penetrated the expansion joints.

I did not continually record site and roost temperatures during the study. Mean monthly temperatures that were used for analysis (Sec. 6.32) were from nearby National Oceanic and Atmospheric Administration weather records at Tombstone station (NOAA, 1980-1993). However, on some occasions I recorded temperatures at a bridge roost (Table 5.1-1) that demonstrate the variability and differences between air temperature on a bridge span and temperature within a roost crevice.

## 5.2 Methods

For most of the 15 consecutive years of this study, I visited the roosts predominantly during June, July, and August. I obtained measurements and other observations of adult females during pregnancy, lactation, and postpartum periods, and I recorded observations of the growth and development of juveniles during the postnatal growth phase until they reached adult size. These visits occurred during the daytime so I could associate juveniles with their mothers and, conversely, identify the young of adult females. Visits made to a maternity roost at night when adult females were gone would probably have caused less disturbance (Burnett and Kunz, 1982), but daytime visits, when adults were present, were essential to obtain mother-young

**Table 5.1-1. Examples of variability in roost temperatures. In 1990, these minimum-maximum ranges of temperature were recorded on a bridge span at SD (approximately 1 m below the roost crevice) and within a roost crevice. Temperatures were recorded with digital maximum/minimum storage thermometers (one thermometer encased and one thermometer on probe). Note that the roost crevice was more variable and could be either cooler or hotter than air temperature on the bridge span. The cooler temperatures after 04 July were probably a result of summer rain storms.**

<b>on Bridge Span</b>	<b>in Roost Crevice</b>
<b>Thermometer left in place from 0930 h on 26 June to 1130 h on 04 July.</b>	
<b>21.9 - 38.6 °C</b>	<b>17.2 - 45.2 °C</b>
<b>Thermometer left in place from 1130 h on 04 July to 0800 h on 07 July.</b>	
<b>21.6 - 27.4 °C</b>	<b>21.3 - 32.9 °C</b>

associations for the types of analysis used in this study. During some years, I visited roosts from May through October to get additional observations before females were heavily pregnant or after summer when adults and grown juveniles were preparing to leave for hibernacula.

More than 300 total visits were made to the roost sites to record data. (Note that just one visit to each of the five colonies x 12 years equals 60 visits). I conducted additional scouting visits occasionally to ensure that bats that were present were safe in the roosts, but I tried not to disturb bats on these visits. Not all roosts were visited every year because some colonies were not present until after the study began, and data for one colony were no longer recorded after the colony was destroyed by vandals. During the first two years and the last six years of the study, I visited all sites less frequently. For example, in 1980, only one visit was made to the *A.p.* colony at SD; in 1990, 3 visits were made to the *A.p.* colony at SD, 2 visits to the *E.f.* colony at SD, 3 visits to *E.f.* at TM, and 3 visits to *E.f.* at TB; but during 1992-1995, only one visit was made to each colony, because I stopped banding new animals that year, and only recaptured females with their young were recorded.

On each visit for which data were recorded, I captured all members of the colony that were present. I removed bats carefully from the crevice in a manner that prevented injury. Bats were placed temporarily into large holding cages until data on individuals were recorded. Following the recording of observations and

measurements of each individual, that individual was placed back into the roost crevice. Rarely, a bat would drop into flight from the crevice after I returned it, but usually, it circled back and re-entered the crevice. When adult females were present with attached young, the mother and young were held in individual containers to validate mother-young associations until observations of them were recorded; then the mother and her young were placed back carefully into the crevice together. I took all of the measurements and other observations of bats. Occasional field assistants (see Acknowledgments) helped only to record data.

All new adult and juvenile females of either species present at the roosts were banded from 1980 through 1992. Most juvenile males and some adult males of both species were also banded (except in 1982, 1991, and 1992 when I had insufficient bands). Bats were banded on the left forearm with aluminum, lipped bat bands with unique numbers. Bands were originally obtained from USFWS supplies (Washington, DC), and later from Gey Band and Tag Company, Inc. (Norristown, PA) and from Lambournes B'Ham, Ltd. (Solihull, West Midlands, England). To prevent wing irritation, bands were checked for rough edges and filed smooth before being placed on a bat. The right forearm was banded only if there were an injury to the left, or if a band on a bat had caused damage. Upon recapture, this alerted me that something had previously happened to the wing of this bat, and I recorded a note about the current state of the wing, so that I could determine whether band injuries had healed.

On each visit I recorded from each individual bat the species, band number, sex, adult/juvenile age class, year, month, day, locality, and comments on unusual body conditions such as extra fat, extra ectoparasites, etc. In addition, reproductive status for adults or growth status for juveniles were included in approximately 70% of the records. Half of the records contained measurements of forearm and body mass. When measurements were recorded, bats were weighed (with the band on) to the nearest 0.01 g on a triple beam balance contained in a large box with an open top and plexiglass window to exclude wind interference. In the first two years, forearms were measured to the nearest mm with a mm ruler. During years 3-15, forearms were measured to the nearest 0.1 mm with Helios steel dial calipers (0.05 mm divisions; Fowler, Germany).

The determination of juvenile (and later, adult) age classification is completely reliable when juveniles are banded and labeled age "0." I labeled new adults banded at unknown age as age " $\geq 1$ " and new bats of questionable juvenile/adult status as age "? 1," but I did not use these two questionable age groupings in analysis of 1-year old bats. During a few years, I took measurements on some young of their un-ossified epiphyses at metacarpal-phalangeal joints by stretching the wing over an illuminated stage of a binocular microscope (Burnett and Kunz, 1982), but these data are not included in this dissertation. I used these un-ossified epiphyses to confirm age "0" but not to confirm age "1". Throughout this paper, "known-age" bats are those first

banded as age 0. "Known-age cohorts" are groups of bats banded at age 0 in the same year. A "yearling" is a bat banded as a known-age juvenile the previous summer.

I recorded the reproductive status of adult females as: "pregnant" (palpation revealed fetal bones), "?pregnant" (slight abdominal bulge and enlarged nipples), "lactating" (milk evident in mammary gland), "post-lactating" (nipples enlarged and scarred, but milk tissue not obvious), "previously having lactated" (nipples scarred and slightly enlarged: this designation meant the bat had lactated in some previous year), "nulliparous" (nipples without scarring and tiny size as in juveniles).

A female removed from the crevice with juveniles attached to her nipples was presumed to be with her own young; there were no cases in which juveniles found with one mother were later found (under natural conditions) with a different mother. This same mother/young specificity was also noted previously for *A. pallidus* (R. Davis, 1969b) and for *E. fuscus* (Kunz, 1974). Juveniles which grabbed onto an adult's nipples during the collection process were noted but not confirmed as her young unless they were found attached to her nipples later.

I recorded growth status of juveniles as: "newborn" (juvenile still attached to mother by umbilical cord or placenta present), "umbilical" (dried umbilical cord still attached and this juvenile assumed to have been born that day; Kunz, 1974; R. Davis, 1969b), "pinkie" (having the same characteristics as an umbilical but without the

umbilical cord and this juvenile presumed born within the previous 24 hours, but not used in analysis as an umbilical unless stated as such).

Two other procedures were performed at these roost sites, but data from them are not addressed in this paper. 1) In 1988 and 1989, some juvenile *A. pallidus* at SD were injected with doubly-labeled water after which blood samples were drawn (Kunz and Nagy, 1988). There was no difference in the survival rate for the treated juvenile females as compared to the untreated juvenile females in each year, so they were retained in the data set for other analysis. (In 1988, return 1989: treated and survive,  $n = 11$ , treated and not survive,  $n = 8$ ; untreated and survive,  $n = 7$ , untreated and not survive,  $n = 3$ ;  $\chi^2 = 0.056$ ,  $0.75 < P < 0.90$ . In 1989, return 1990: treated and survive,  $n = 8$ , treated and not survive,  $n = 4$ ; untreated and survive,  $n = 7$ , untreated and not survive,  $n = 7$ ;  $\chi^2 = 0.211$ ,  $0.50 < P < 0.75$ .)

2) In 1985, I removed 10 juvenile female *A. pallidus* from SD and 5 juvenile female *A. pallidus* from TB in early October, because I hypothesized that these might be some of the young bats that would not survive winter since they had low body mass and were still present after adults had already left for hibernation. These juveniles were held captive for eight days and fed artificially until their body masses had increased before release. (No controls were performed, so the experiment is not reported.) The survival rate for the diet-enhanced females did not differ significantly from untreated females, so they were retained in the data set for other analyses.

(Enhanced and survived,  $n = 14$ , enhanced and not survive,  $n = 1$ ; untreated and survived,  $n = 10$ , untreated and not survive,  $n = 1$ ;  $\chi^2 = 0.053$ ,  $0.75 < P < 0.90$ .)

The productivity in 1986 of the diet-enhanced females also did not differ significantly from untreated females. (Enhanced and reproduced,  $n = 12$ , enhanced and not reproduce,  $n = 3$ ; untreated and reproduced,  $n = 8$ , untreated and not reproduce,  $n = 3$ ;  $\chi^2 = 0.189$ ,  $0.50 < P < 0.75$ .)

The few bats to which I thought I had caused physical harm were excluded totally from any data analysis. I also did not include a few bats that I released alive that I know remained alive after rehabilitation. For example, in data analysis, I treated the *A. pallidus* colony at TB as being totally absent after its destruction by workers in 1989 (see Sec. 6.34; the *E. fuscus* colony was in a separate expansion joint and was not similarly affected), because I know the five survivors could not have lived without my intervention. (Three of five adult females that I treated returned the following year and had young, and these offspring and their offspring continued to return until 1992, but none of these bats are used in data analysis.)

Bats that were known to have been harmed by people (other than myself) at these roost sites were retained in the data set for analysis, because this study is about survival of bats that roost part of the year in man-made structures; thus, mortality that is human-caused is part of the possible mortality factors existing at these roost sites. However, in analyses such as mean survivorship, I did not include zero-value

data from the TB colony of *A. pallidus* after its destruction, because it would excessively influence results and interpretation of the data.

Only female bats return reliably to these maternity roosts, so only females were analyzed in this study for survival rates (see Results, Sec. 6). Return rates were much higher when only true colony members, and not transients, were included. "True colony members" are the adult females that actually give birth to their young at the roost, and/or they are the females that were born at the roost. "Transients" are the females who were not born and/or did not give birth at these roosts. The data set used to determine survival rates was modified to include only those females who gave birth or were born at the roost sites. This greatly improved the reliability of estimates of survival.

For analysis of survival data, the following assumptions were made.

Assumption 1) For both species, a missing bat was one that had not survived. If, in reality, a missing bat was actually alive and had simply not returned, the calculated survival rate was underestimated. Among the evidence in support of Assumption 1 was the fidelity to these roost sites demonstrated by homing experiments in previous studies. Females of both species of bats returned to the Tombstone bridge roosts during experiments in which they were not only harassed during capture, but they were physically taken away from the roost and released at distant points (R. Davis, 1966). For example, a banded female pallid bat was removed repeatedly from the SD

roost in 1960 between late May and mid September, taken to eight locations in six distinctly different directions at distances of 33-109 km, and after each release she returned to SD--in each case within 21 days or less (R. Davis and Cockrum, 1962a). A second example showed the fidelity of *E. fuscus* females to these roosts when 46 females were taken in August 1961 from TM, released 169 km away, and 15 of them returned the following Spring (R. Davis, 1966). A third example, again for *A. pallidus* (again R. Davis, 1966), was the removal of 13 females from SD in July 1959 to a release point 528 km away; one female returned within a month, and a second female returned the following Spring.

But most importantly, no females in the present study who were "true colony members" were found again after having failed to be present at some time during one year. Exceptions were at SD where disturbance of some sort caused many females to disappear during 1982 and 1983, before they again were present. Some other error in survival estimates was probably caused by my schedule of fewer visits in the last four years of the study, because some bats that could actually have been alive may have been missed, and survival rates also would be underestimated.

Assumption 2) There was no loss of bands. The bands were fairly permanent. (In fact, they were found still attached to skeletal carcasses, and even on a separated forelimb of a dead animal.) The exception was for neonates when a band could slide off their pliable fingers. However, when this happened the problem was usually

rectified: the band fell below the roost, an unbanded baby was found attached to a mother that the records showed had a banded young previously, and that young was missing; if the sex and larger size of the baby were appropriate, the baby was rebanded. This was a rare event; babies were nearly always recaptured with their bands on.

Another exception was a bigger source of potential error: the loss of a band that I didn't know about. This was an unknown amount of error and also caused an underestimate of survival. A further type of band loss was one in which the band became illegible. But because of the frequency of visitation to these roosts, I usually was able to change problematic bands before a number became totally illegible. If not corrected, however, this also would cause underestimation of survival.

Assumption 3) This study did not disturb the bats, nor did it cause some to abandon the roost. This assumption was definitely in error. While other survival studies of bats simply ignored this issue, I addressed it statistically (see Sec. 6.34).

A different potential source of error when working with demographics of populations may occur as a result of the technique used in estimating the size of the population. In this study, however, population size was not estimated. It was determined directly by counts of captured bats, because, with few exceptions, all members of a colony were captured on each visit.

Life table analysis follows Caughley (1977) for known-age cohort analysis. Data were analyzed using SigmaStat statistical software for Windows 3.1 from Jandel Scientific (Fox et al., 1994). Tests were used only if the data met assumptions for those tests, e.g., meeting normality and variance tests before applying *t*-tests and regressions analyses. Yates correction factor was used for all  $\chi^2$  analyses with *d.f.* = 2, unless absolute value of  $(f_{11} \times f_{22} - f_{21} \times f_{12}) \leq n/2$  (Zar, 1974).

Scientific names follow Jones et al. (1991).

Permits for scientific collecting and holding were obtained each year from the Arizona Game and Fish Department (Phoenix, AZ).

## 6. RESULTS AND DISCUSSION

Between 1980 and 1992, 1702 *A. pallidus* and 2231 *E. fuscus* were banded (Figure 6-1). After the first year of banding at a particular roost, most of the new individuals banded in subsequent years were juveniles. The decrease in *A. pallidus* bandings at TB from 1989-1992 was due to colony destruction in early 1989. The increased number of bandings of *E. fuscus* at SD and TB from 1981-1984 was the result of new colony establishment at those sites.

Recaptures (1981-1995) brought the total of records to 11,342 *A. pallidus* and 13,849 *E. fuscus*.

Return rates of all banded bats demonstrated that only adult females and grown juvenile females reliably returned to these maternity roosts (Figure 6-2). Return rates of males of both species indicated that they do not faithfully return to these roosts after they leave this natal roost for their first winter; therefore, it was not possible to determine survival rates for males of either species at these roosts. The return rates were lower than the survival rates that will be presented later, because transient bats that do not reliably return were included in return rates.

Once colonies became established, the number of true colony members of adult females did not vary much from year to year (Table 6-1). Increase in overall size of colonies was due to survival of juvenile females. The decreases at all roosts in

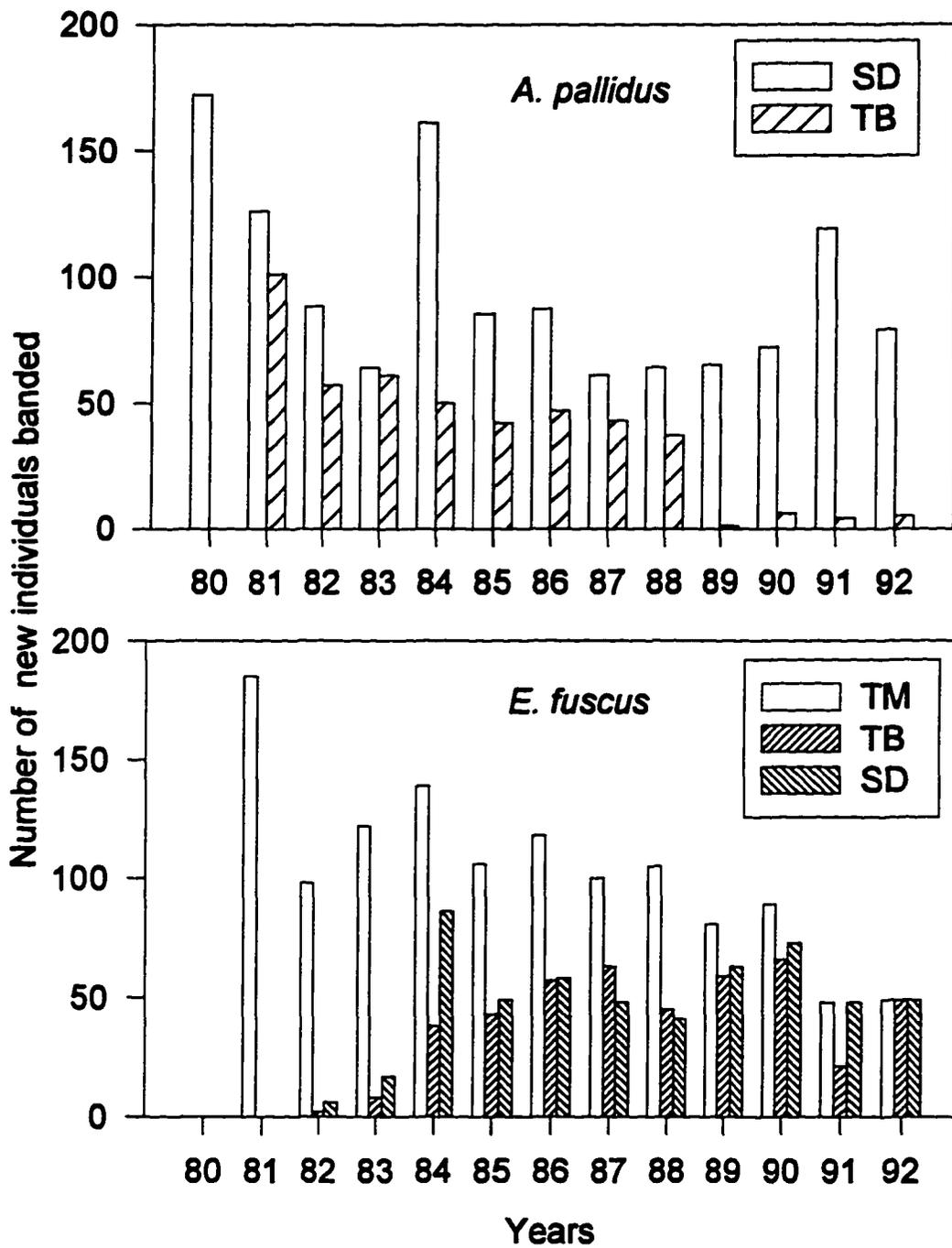


Figure 6-1. Numbers of *A. pallidus* and *E. fuscus* banded each year at each locality.

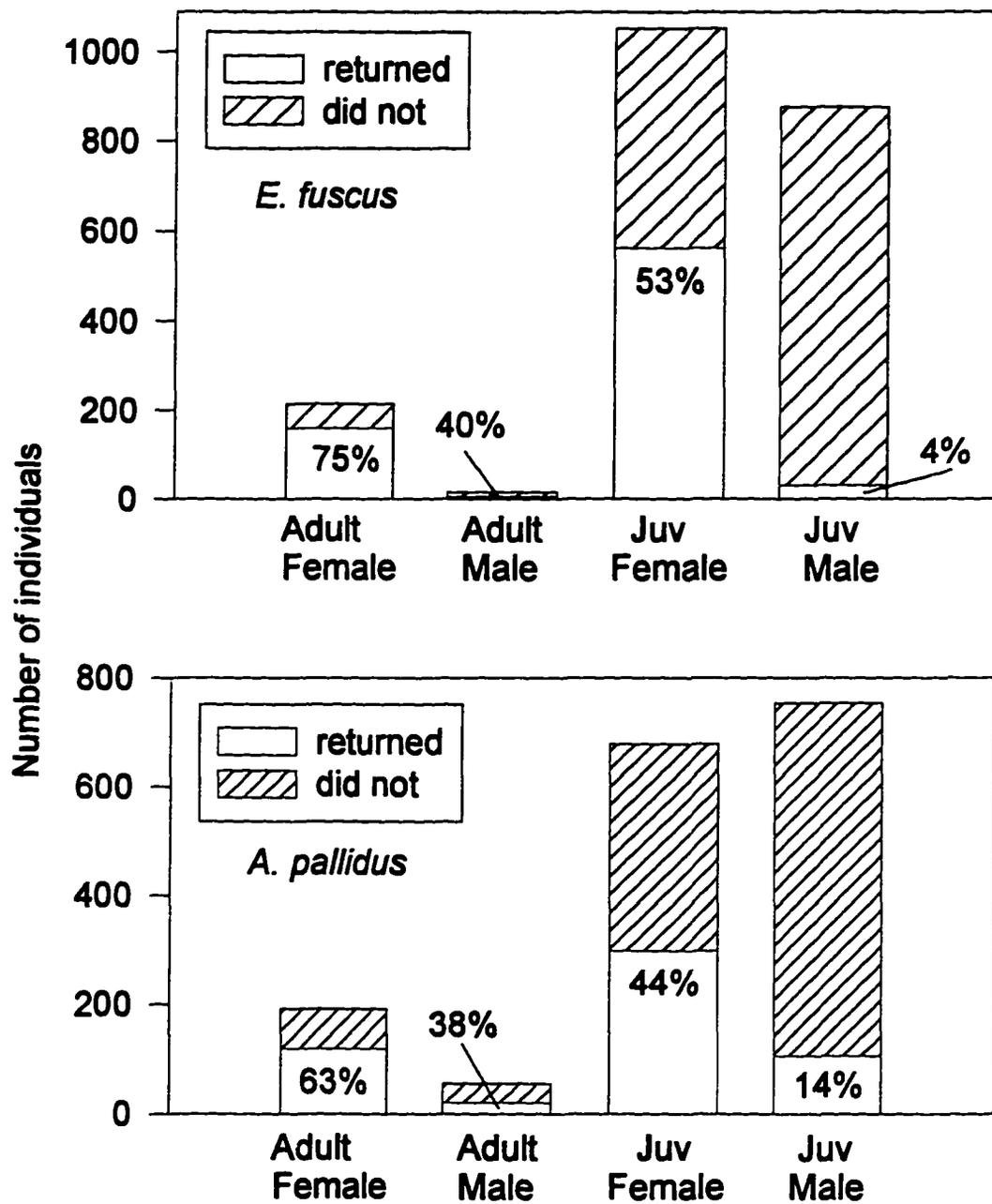


Figure 6-2. Return rates of all banded *A. pallidus* and *E. fuscus*, by sex and age class, from 1980-1992. Transient animals that do not return faithfully to the roosts were included in these analyses.

Table 6-1. The dynamics of colony sizes. Numbers are adult females that were "true colony members" (see Methods). Numbers enclosed by parentheses indicate adult females of the group which were not newly banded that year. Note that the difference between the two numbers was usually small and that there were few new adult females at a roost each year. Mean colony size includes year \* through 1993 except *Ap* at TB.

Year	<i>E. fuscus</i>			<i>A. pallidus</i>	
	TM	TB	SD	TB	SD
1980	--	--	--	--	74
1981	77	none	--	34	90* (85)
1982	107* (73)	2 (2)	6	36 *(36)	85 (83)
1983	121 (119)	13 (11)	21	45 (45)	32 (32)
1984	119 (115)	31* (27)	43* (23)	41 (41)	74 (68)
1985	110 (108)	49 (49)	45 (45)	25 (25)	40 (39)
1986	105 (105)	59 (59)	42 (41)	29 (29)	42 (42)
1987	95 (95)	62 (62)	43 (43)	30 (30)	33 (33)
1988	111 (110)	55 (55)	43 (43)	27 (27)	38 (38)
1989	97 (96)	59 (59)	59 (59)	--	40 (40)
1990	94 (94)	64 (63)	74 (74)	3 (3)	43 (42)
1991	106 (106)	51 (49)	86 (86)	4 (4)	60 (45)
1992	126 (125)	64 (59)	110 (110)	4 (4)	52 (52)
1993	154 (154)	75 (75)	119 (116)	3 (3)	64 (64)
1994	139 (137)	62 (62)	76 (74)	0	51 (51)
1995	93 (93)	47 (47)	79 (77)	0	74 (32)
Mean	112	57	66	33	53
(SE)	(4.8)	(3.7)	(9.3)	(2.8)	(5.4)

1994 and 1995 were due, at least in part, to my having missed bats because I only visited roosts once each in those years.

## 6.1 Life tables and survivorship curves from known-age cohorts

### 6.11 Life tables and curves from individual cohorts

*Life tables.*-- I provide age-specific life tables for individual cohorts of both *A. pallidus* and *E. fuscus* (Appendix B). These are the first life tables reported for *A. pallidus* and for western populations of *E. fuscus*. Each table represents an entire cohort that was banded at juvenile age, and for which the surviving members were noted in all subsequent years. Life tables were prepared for each known-age cohort of *A. pallidus* at each roost from 1980 through 1988 (the TB roost was destroyed in 1989) and for SD through 1992. Life tables for *E. fuscus* at TM are from 1981-1982, then from 1983-1992, the colony of *E. fuscus* at TM was combined for analysis with the new colony at TB because some individual bats moved between these two roosts. Life tables for *E. fuscus* at SD are for 1984-1992.

During 15 consecutive years of study, survivorship within and between populations of *A. pallidus* and *E. fuscus* varied considerably at the Tombstone roosts. Mean first-year survivorship was significantly higher for known-age cohorts of *E. fuscus* than for *A. pallidus* (*Ef*:  $n = 21$ ,  $\bar{x} = 0.56$ ,  $SE = \pm 0.03$ , range = 0.30-0.77, *Ap*:  $n = 20$ ,  $\bar{x} = 0.46$ ,  $SE = \pm 0.04$ , range = 0.18-0.74;  $t = -2.09$ , *d.f.* = 39,  $P = 0.043$ ).

Analysis of known-age cohorts showed that survival was age-dependent for both species. After the first year of age, annual mortality rates tended to remain low until about age 4-5 years for *A. pallidus* or age 6-8 years for *E. fuscus*, when mortality again increased. Exceptions to high mortality in old age were cases when only one or two old bats in a cohort remained alive for several consecutive years; mortality rates remained at zero until those bats died.

Second-year survivorship was significantly higher than first-year survivorship for both species. (*Ap*: Mann Whitney rank sum test,  $T = 506.5$ ,  $n = 19, 20$ ,  $P < 0.0001$ . *Ef*: Student's  $t = -5.84$ ,  $d.f. = 40$ ,  $P < 0.0001$ .) *Eptesicus fuscus* had significantly higher survivorship than *A. pallidus* for the second age class also. (Second year, *E. f.*:  $n = 21$ ,  $\bar{x} = 0.80$ ,  $SE = \pm 0.03$ , *A. p.*:  $n = 19$ ,  $\bar{x} = 0.66$ ,  $SE = \pm 0.04$ ; Mann Whitney rank sum test,  $T = 285.0$ ,  $n = 19, 20$ ,  $P = 0.005$ ). Survivorship of *E. fuscus* for the third age class was higher than for *A. pallidus* but not significantly so (*E. f.*:  $n = 21$ ,  $\bar{x} = 0.80$ ,  $SE = \pm 0.02$ , *A. p.*:  $n = 18$ ,  $\bar{x} = 0.78$ ,  $SE = \pm 0.04$ ; Mann Whitney rank sum test,  $T = 325.5$ ,  $n = 18, 21$ ,  $P = 0.338$ ).

In comparison to earlier studies of the eastern subspecies (Table 4-1), the higher survival values for *E. fuscus* in the current study may be a real characteristic of western populations, or they may have resulted from two consequences of the colonies being well-studied: 1) transients were identified and not included in analysis,

and 2) there were more visits to determine whether an individual was still alive rather than counting it dead because it had been missed. Besides the contrast in length of study, an important difference in methods between the Mills et al. (1975) study and mine was that only a sample of the cohort was captured in the Mills study; thus, it is extremely likely that they included transient bats that were less likely to return, and as a result the survival rate was undoubtedly underestimated.

There are no other survival studies of *A. pallidus* with which to compare the results here, however, interspecific comparisons are possible. Juvenile survival rates for other vespertilionid bats, *E. fuscus*, *Nycticeius humeralis*, *Plecotus townsendii*, and *Myotis grisescens* (Table 4-1), ranged from 10.5-58.6%, so the findings here of juvenile survival rates of 18-74% for *A. pallidus* (Appendix B) agree reasonably well with survival rates for other species in the family.

The period of time covered in the life tables contains the maximum recorded life span for *A. pallidus* and approaches the maximum recorded life span of *E. fuscus* (Appendix B). The tables for *A. pallidus* are incomplete for cohorts from the later years, and most of the tables of *E. fuscus* are incomplete, because the life span of these bats is longer than the years of study. Life tables from some of the unknown-age adult cohorts (Appendix C) are available for comparison with other studies in which life tables were prepared from "banding-time-specific" rather than age-specific cohorts (Keen, 1988).

*Survivorship curves.*-- For ease of comparison between and within species, I prepared survivorship curves from *lx* schedules rather than mortality schedules of the life tables (Appendix B), because survivorship values for all cohorts begin at the same value of 1.0 (Caughley, 1977).

In some years, like 1982, there was high survivorship from juvenile to yearling age for both cohorts of *A. pallidus* at SD and TB as well as for the colony of *E. fuscus* at TM (Figure 6.11-1). In comparison, the survivorship of both cohorts of *A. pallidus* from 1984 was extremely low, as was the survivorship of both cohorts of *E. fuscus* in 1984 (Figure 6.11-2). Reasons for year-to-year variation in survivorship are discussed in Sec. 6.3.

#### 6.12 Mean survivorship tables and curves from multiple cohorts

Because the annual estimates of survival for both species are presumed to be a random sample of some overall population survival rate with variation potentially produced by randomly varying environmental factors, the rates may be averaged (Keen, 1988). For the present study, therefore, I combined years to yield mean survivorship data for the separate colonies of *A. pallidus* at SD or TB, and of *E. fuscus* at SD or TM-TB (Tables 6.12-1, 6.12-2, 6.12-3, 6.12-4; Figure 6.12-1).

Average life expectancy is the average age at which members of a cohort die and cannot be determined until all cohort members have died (Keen, 1988). Because many cohorts in this study had members alive at the conclusion of the study, it was

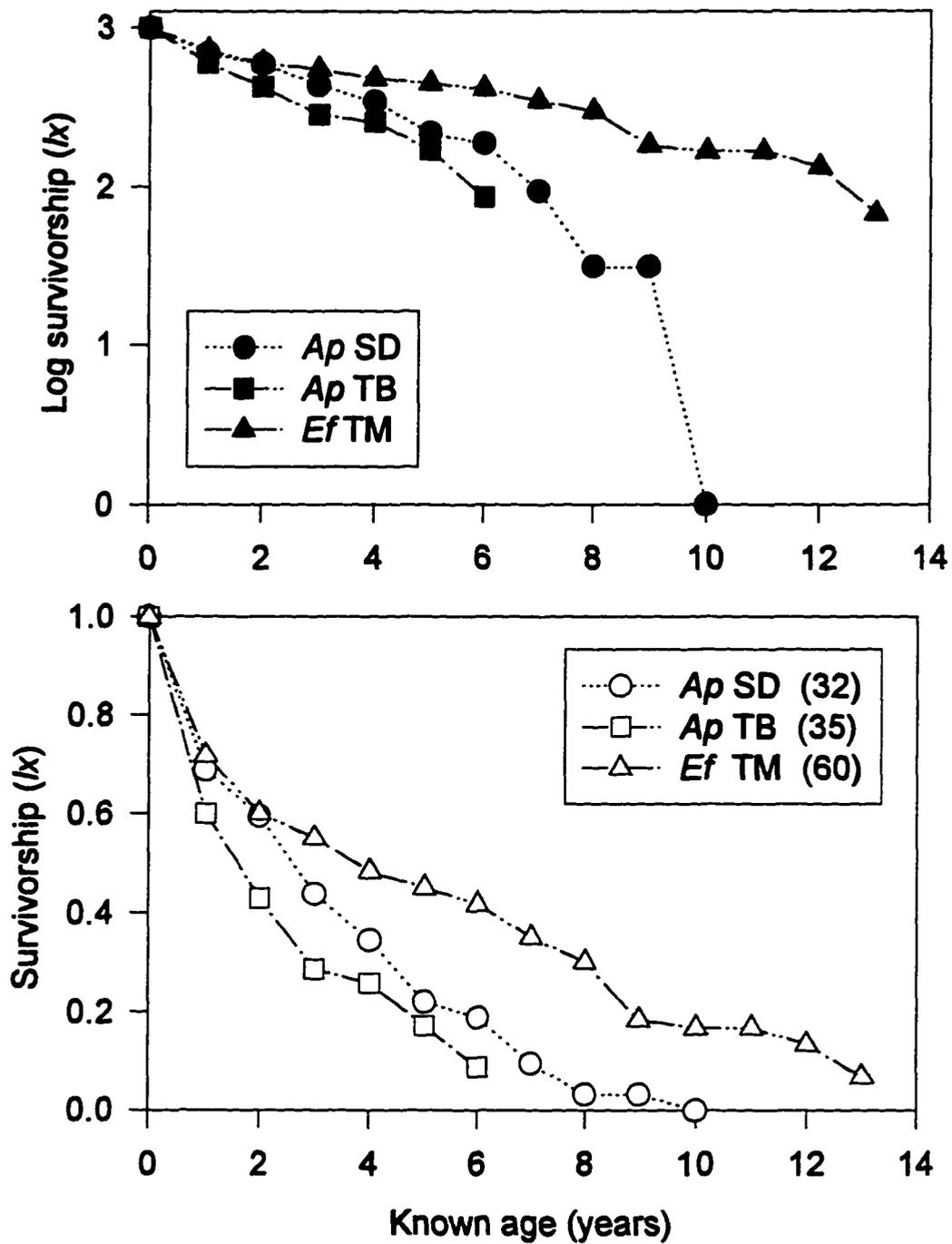


Figure 6.11-1. Survivorship curves of *A. pallidus* and *E. fuscus* from individual known-age cohorts in 1982. Initial sample size of cohorts is given in parentheses. Top graph is a semilog plot of the same data in the bottom graph.

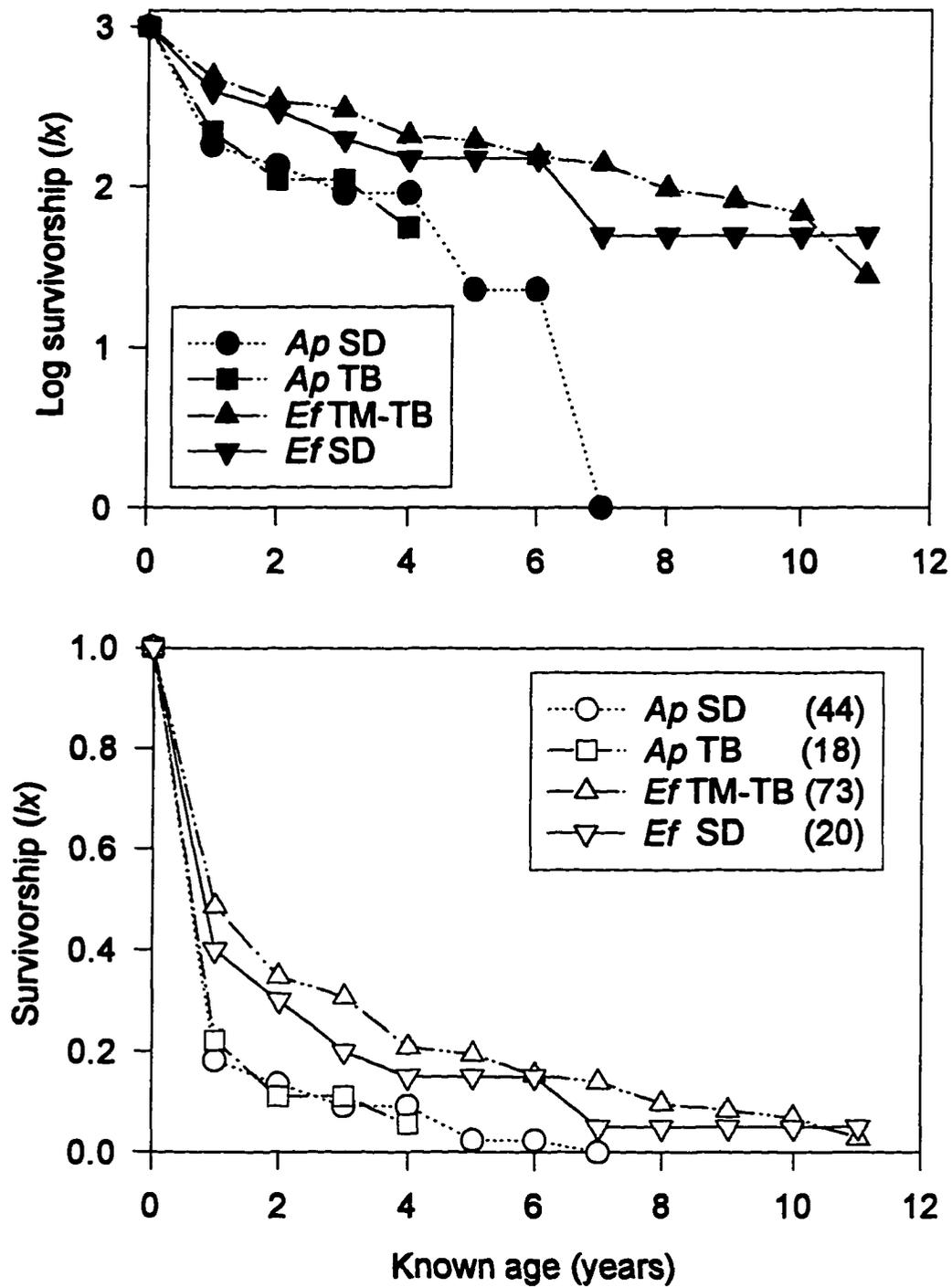


Figure 6.11-2. Survivorship curves of *A. pallidus* and *E. fuscus* from individual known-age cohorts in 1984. Initial sample size of cohorts is given in parentheses. Top graph is a semilog plot of the same data in the bottom graph.

Table 6.12-1. Mean survivorship of female *A. pallidus* at SD, 1980-1995. CYr is the cohort and year of banding of juvenile females banded at known age 0. Total for each Cohort Age Class is the sum of Number Surviving Cohort Members of all cohorts. Mean Survival is the proportion of the Total of Number Surviving Cohort Members for each Cohort Age Class compared to the Total of the 0 Cohort Age Class or compared to the CT (cumulative total) of the 0 Cohort Age Class if the study ended before all members of a cohort died (vertical bars indicate where the study ended in 1995). \*  $\pm$ SE of Mean Sur. is one SE for the number of CYr below. Srv. Rate (survival rate) is the proportion of the Total of Number Surviving Cohort Members for each Cohort Age Class compared to the previous age class, or the CT of the previous Age Class up to that point if the study ended before all cohort members died.\*\* See examples below for \* and \*\*.

		Cohort Age Class (years)										
		0	1	2	3	4	5	6	7	8	9	10
$\bar{x}$	Survival	1.00	0.49	0.34	0.25	0.18	0.11	0.08	0.04	0.01	0.01	0
$\pm$	SE $\bar{x}$ Sur.	0	0.04	0.04	0.03	0.03	0.02	0.02	0.02	0.01	0.01	--
	Srv. Rate	1.00	0.49	0.69	0.72	0.73	0.59	0.76	0.52	0.29	1	0

CYr	CT	Number of Surviving Cohort Members										
80	--	50	37	27	12	10	3	2	1	0	--	--
81	--	28	12	10	10	4	3	1	0	--	--	--
82	--	32	22	19	14	11	7	6	3	1	1	0
83	--	28	13	1	1	1	1	0	--	--	--	--
84	--	44	8	6	4	4	1	1	0	--	--	--

Table 6.12-1 - Continued

85	--	23	13	8	6	5	4	4	1	1	1	0
86	230	25	6	5	3	1	0	--	--	--	--	--
87	260	30	15	8	6	5	3	2	2	0	--	--
88	289	29	18	13	10	6	6	5	4		--	--
89	320	31	15	10	10	7	6	5		--	--	--
90	355	35	14	11	10	10	4		--	--	--	--
91	390	35	16	11	8	5		--	--	--	--	--
92	432	42	24	19	12		--	--	--	--	--	--
Total		432	213	148	106	69	38	26	11	2	2	0

\* Example 1: When the study ended before all cohort members had died (vertical bars), the Mean Survival is the total of Number of Surviving Cohort Members for that Age Class divided by the CT up to that point. For Cohort Age Class 5, Mean Survival is 38 divided by 355 = 0.11.

\*\* Example 2: The Srv. Rate is the total of Number of Surviving Cohort Members for that Age Class divided by the Total of the previous Age Class up to that point. For Cohort Age Class 5, Srv. Rate is 38 divided by 64 (not 69) = 0.59.

Table 6.12-2. Mean survivorship of female *A. pallidus* at TB, 1981-1990. CYr is the cohort and year of banding of juvenile females banded at known age 0. Total for each Cohort Age Class is the sum of Number Surviving Cohort Members of all cohorts. Mean Survival is the proportion of the Total of Number Surviving Cohort Members for each Cohort Age Class compared to the Total of the 0 Cohort Age Class or compared to the CT (cumulative total) of the 0 Cohort Age Class if the cohort life span was interrupted; vertical dashed lines indicate where each cohort was affected when the colony was destroyed (number of survivors to the right of the dashed line is not used in calculations).  $\pm$ SE of Mean Sur. is one SE for the number of CYr below. Srv. Rate (survival rate) is the proportion of Total or CT of Number Surviving Cohort Members for each Cohort Age Class compared to the previous age class up to that point. See Table 6.12-1 for examples: Mean Survival and Srv. Rate calculations.

		Cohort Age Class (years)								
		0	1	2	3	4	5	6	7	8
$\bar{x}$	Survival	1.00	0.42	0.29	0.2	0.13	0.1	0.07	0.04	—
$\pm$ SE	$\bar{x}$ Sur.	0	0.06	0.06	0.04	0.05	0.04	0.02	—	—
	Srv. Rate	1.00	0.42	0.67	0.71	0.74	0.69	0.5	1	—

CYr	CT	Number of surviving cohort members								
81	23	23	10	7	5	3	2	1	1	0
82	58	35	21	15	10	9	6	3	1	0
83	86	28	5	2	2	1	1	0	—	—
84	104	18	4	2	2	1	0	—	—	—
85	123	19	11	8	5	1	0	—	—	—
86	140	17	9	6	1	0	—	—	—	—
87	165	25	9	3	0	—	—	—	—	—
88	182	17	1	0	—	—	—	—	—	—
89	—	—	—	—	—	—	—	—	—	—
	Total	182	69	40	24	14	9	4	1	—

Table 6.12-3. Mean survivorship of female *E. fuscus* at TM-TB, 1981-1995. CYr is the cohort and year of banding of juvenile females banded at known age 0. Total for each Cohort Age Class is the sum of Number Surviving Cohort Members of all cohorts. Mean Survival is the proportion of the Total of Number Surviving Cohort Members for each Cohort Age Class compared to the Total of the 0 Cohort Age Class or compared to the CT (cumulative total) of the 0 Cohort Age Class if the study ended before all members of a cohort died (vertical bars indicate where the study ended in 1995).  $\pm$ SE of Mean Sur. is one SE for the number of CYr below. Srv. Rate (survival rate) is the proportion of Total or CT of Number Surviving Cohort Members for each Cohort Age Class compared to the previous age class up to that point. See Table 6.12-1 for examples of Mean Survival and Srv. Rate calculations.

		Cohort Age Class (years)														
		0	1	2	3	4	5	6	7	8	9	10	11	12	13	14
$\bar{x}$ Survival		1.00	0.53	0.43	0.36	0.28	0.23	0.19	0.16	0.13	0.09	0.08	0.07	0.06	0.04	0
$\pm$ SE $\bar{x}$ Sur.		0	0.03	0.04	0.03	0.04	0.03	0.03	0.03	0.03	0.02	0.02	0.03	0.04	0.04	--
Srv. Rate		1.00	0.53	0.82	0.82	0.8	0.84	0.86	0.86	0.8	0.71	0.89	0.77	0.73	0.44	--
CYr	CT	Number of Surviving Cohort Members														
81	--	47	14	12	9	7	6	5	4	3	2	2	1	1	0	--
82	107	60	43	36	33	29	27	25	21	18	11	10	10	8	4	--
83	171	64	32	25	20	15	12	10	8	6	6	5	4	2	--	--
84	243	72	35	25	22	15	14	11	10	7	6	5	2	--	--	--
85	310	67	32	20	16	11	8	8	7	5	3	3	--	--	--	--

Table 6.12-3 - *Continued*

86	376	66	29	25	21	16	14	14	12	10	7	--	--	--	--	--
87	448	72	36	24	18	10	10	9	9	8		--	--	--	--	--
88	517	69	30	25	19	16	16	15	12			--	--	--	--	--
89	572	55	33	28	26	23	18	11				--	--	--	--	--
90	653	81	44	41	37	34	23					--	--	--	--	--
91	718	65	36	35	30	24						--	--	--	--	--
92	793	75	54	48	32							--	--	--	--	--
<b>Total</b>		793	418	344	283	200	148	108	83	57	35	25	17	11	4	--

Table 6.12-4. Mean survivorship of female *E. fuscus* at SD, 1984-1995. CYr is the cohort and year of banding of juvenile females banded at known age 0. Total for each Cohort Age Class is the sum of Number Surviving Cohort Members of all cohorts. Mean Survival is the proportion of the Total of Number Surviving Cohort Members for each Cohort Age Class compared to the Total of the 0 Cohort Age Class or compared to the CT (cumulative total) of the 0 Cohort Age Class if the study ended before all members of a cohort died (vertical bars indicate where the study ended in 1995).  $\pm$ SE of Mean Sur. is one SE for the number of CYr below. Srv. Rate (survival rate) is the proportion of Total or CT of Number Surviving Cohort Members for each Cohort Age Class compared to the previous age class up to that point. See Table 6.12-1 for examples of Mean Survival and Srv. Rate calculations.

		Cohort Age Class (years)											
		0	1	2	3	4	5	6	7	8	9	10	11
$\bar{x}$ Survival		1.00	0.64	0.53	0.43	0.32	0.28	0.25	0.16	0.12	0.08	0.05	0.05
$\pm$ SE $\bar{x}$ Sur.		0	0.05	0.06	0.05	0.04	0.05	0.04	0.05	0.04	0.03	0.01	--
Srv. Rate		1.00	0.64	0.83	0.8	0.79	0.88	0.82	0.79	0.9	0.8	1	1

CYr	CT	Number of Surviving Cohort Members											
84	20	20	8	6	4	3	3	3	1	1	1	1	1
85	37	17	7	3	2	2	1	1	1	1	1	1	--
86	50	13	7	5	4	4	4	3	3	3	2	--	--
87	73	23	11	11	9	8	8	7	5	4	--	--	--

**Table 6.12-4 - Continued**

<b>88</b>	<b>92</b>	<b>19</b>	<b>14</b>	<b>10</b>	<b>9</b>	<b>8</b>	<b>6</b>	<b>5</b>	<b>5</b>	<b>--</b>	<b>--</b>	<b>--</b>	<b>--</b>
<b>89</b>	<b>126</b>	<b>34</b>	<b>26</b>	<b>24</b>	<b>20</b>	<b>17</b>	<b>16</b>	<b>12</b>	<b>--</b>	<b>--</b>	<b>--</b>	<b>--</b>	<b>--</b>
<b>90</b>	<b>151</b>	<b>25</b>	<b>18</b>	<b>14</b>	<b>12</b>	<b>7</b>	<b>5</b>	<b>--</b>	<b>--</b>	<b>--</b>	<b>--</b>	<b>--</b>	<b>--</b>
<b>91</b>	<b>169</b>	<b>18</b>	<b>13</b>	<b>11</b>	<b>8</b>	<b>5</b>	<b>--</b>						
<b>92</b>	<b>215</b>	<b>46</b>	<b>34</b>	<b>31</b>	<b>24</b>	<b>--</b>							
	<b>Total</b>	<b>215</b>	<b>138</b>	<b>115</b>	<b>92</b>	<b>54</b>	<b>43</b>	<b>31</b>	<b>15</b>	<b>9</b>	<b>4</b>	<b>2</b>	<b>1</b>

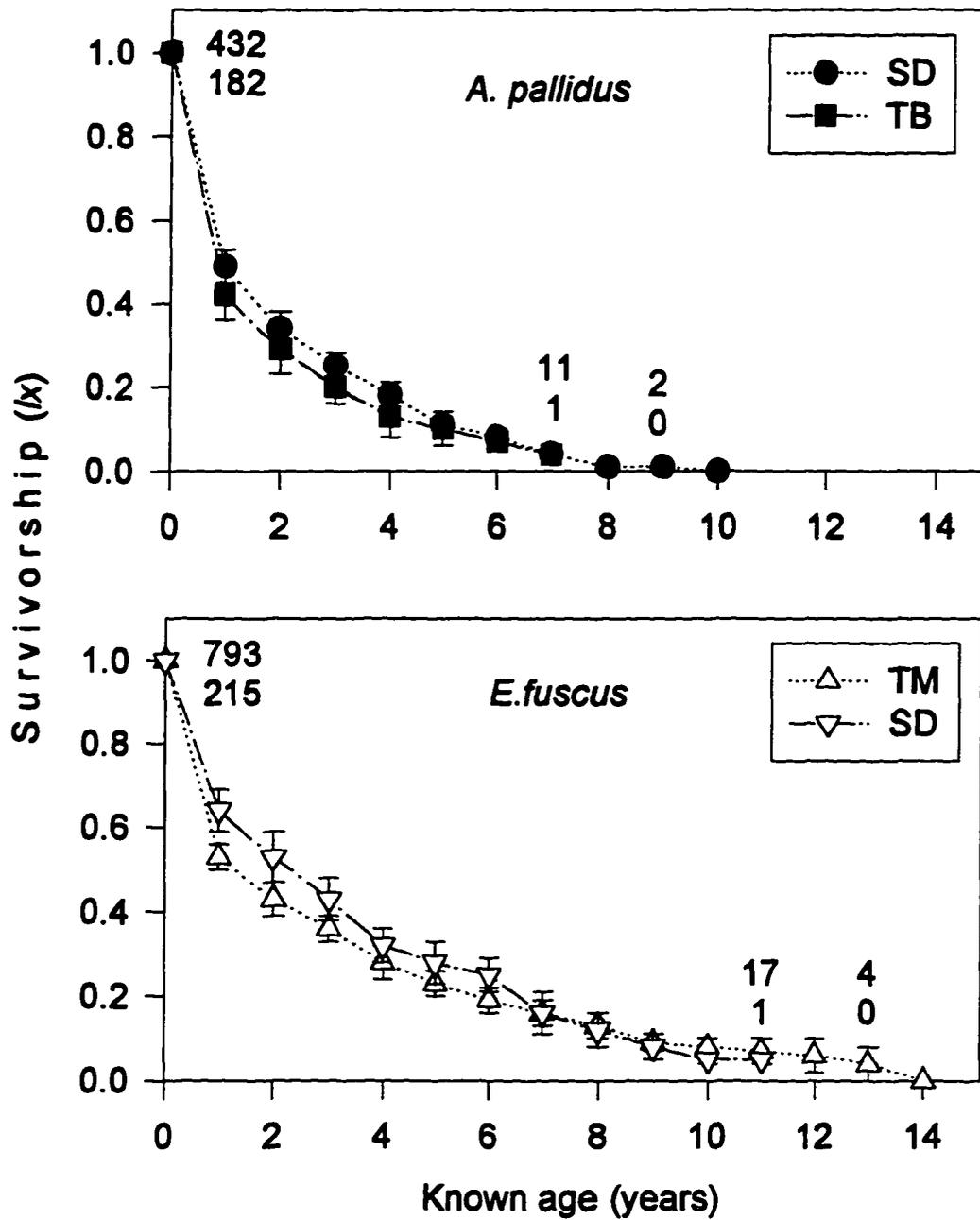


Figure 6.12-1. Mean survivorship curves from pooled known-age cohorts of female *A. pallidus* and *E. fuscus*. Bars equal  $\pm 1$  SE. Sample sizes are given for the juvenile and two older age classes.

practical to use a "median life expectancy," the age by which 50% of the population had died. Median life expectancy was less than one year for *A. pallidus* and slightly more than one year for colonies of *E. fuscus* (Figure 6.12-1).

Throughout the present study, averaged survivorship was higher for colonies of *E. fuscus* than for colonies of *A. pallidus* (Tables 6.12-1 to 6.12-4). These differences in life history, of survival rates and longevity, between the two species of bats that share the same macro-environmental conditions at their maternity roosts, permit both species to maintain relatively stable populations through time.

For obvious reasons, there have not been many long-term survivorship studies of vertebrates (Clutton-Brock, 1988). This is true for bats as well (Keen, 1988). My primary purpose for collecting the data and preparing life tables with age-specific survival and mortality rates was to contribute to the knowledge of the attributes that define a population (for example, the death rate or the sex ratio), in order to determine the factors that regulate populations through time. These attributes are most useful when they are specific for age, because the values change with the proportions of age groups in the population (Caughley, 1977). Age-specific mortality can be studied simply to further knowledge of how populations of certain species change through time; for instance, is survival age-dependent in a population? Age-specific mortality can be used to compare different populations of the same species or different species; rates can be determined for each population or each age group

within the population and directly compared. And age-specific mortality can also be used in applied wildlife management or wildlife conservation.

## 6.2 Longevity

When this study began in August 1980 at the SD roost, an adult male pallid bat was recaptured that had been banded there as a juvenile in 1970 (R. Davis, pers. comm.); thus, the bat was 10 years old. This was a new record longevity for *A. pallidus*.

During the present study, a female *A. pallidus* banded at SD as an adult of unknown age in 1980 survived to 1990. She was at least 11 years of age, and represents another longevity record for *A. pallidus* (Appendix C.1).

Only one other bat from earlier years of research activity was observed at any of the Tombstone roosts during the present study—a female *A. pallidus* that had been banded as a juvenile at SD in 1973 was also recaptured there in 1980 (thus, she was seven years old). This female and the record-holding male above were not observed again in any later years.

The report by Davis (1986) of a 20-year old male *E. fuscus* in Arizona demonstrated a big increase in our knowledge of maximum longevity in this species since the previous record for western populations was only half that age (Cockrum, 1973). But even during my study of this species, 37 females reached at least 11

years, 28 reached 12 years, 15 reached 13 years, 3 reached at least 14 years (Appendices B and C), and the oldest *E. fuscus* in this study was a female at least 15-years old who was still alive when the study ended (Appendix C.2).

The most recently published list of maximum longevity records for bats included 41 species ranging from an unimpressive 2.1 years to an amazing 30 years (Tuttle and Stevenson, 1982), and suggests that there is tremendous variation in potential life span of the Chiroptera. As more records accumulate, however, it becomes apparent that much of the picture is still missing for many species. For example, the record of 30 years is for one of the most common species of bats in the U.S., *Myotis lucifugus*, a colonial species that roosts in large aggregations in sites accessible to biologists who can then band and recapture huge samples (Keen and Hitchcock, 1980). The species on the list with the shortest life span is a solitary, tree-dwelling species, *Lasiurus cinereus*, for which a recapture of the few that have been banded is rare. Another species of tree dwelling bat, *Lasionycteris noctivagans*, has recently been added to the list with a record longevity of just four years (Perkins, 1994). Other notable new records that have been published recently for free-living bats include *Rousettus leschenaulti* at 14 and *Megaderma lyra* at 13 years (Badwaik, 1992), *Myotis yumanensis* at 14 years (Boutin and Willis, 1996), *Plecotus townsendii* at 21 years (Perkins 1994), and the latest update (Davis and Hitchcock, 1995) on *M. lucifugus* is now 34 years of age!

The reasons for the extremely high values of life span for bats, as compared to allometric predictions for most mammals in which life span is usually a linear function of body mass or brain mass (Jürgens and Prothero, 1987), are not clear, and life span of bats may not scale with body size at all (Calder, pers. comm.). To paraphrase questions from Calder (1985) on long life span of hummingbirds--is the long life span of bats due to lower vulnerability throughout life, or do bats age at a lower rate than other mammals?

Records of longevity should not be discarded as little more than interesting trivia about exceptional animals in a population because they do provide clues to population life span, but these records are not a measure of average survival and life span (Keen, 1988). Rather, age-specific cohort analysis is necessary to determine these population life history characters. There is no question that mean longevity within a population, along with survivorship, are two of the major traits that define the life history of a species and may provide clues to other attributes as well. In Great Britain, for example, a long-term study of *Rhinolophus ferrumequinum* has shown that female lifetime reproductive success is strongly correlated with life span (Ransome, 1995).

### 6.3 Factors influencing first-year survivorship

The first-year survivorship values of individual known-age cohorts of *A. pallidus* and *E. fuscus* (Appendix B) revealed considerable variation within and between species and between roosts for the 12 years that data were available (Figures 6.3-1 and 6.3-2). The cohorts of *A. pallidus* at SD and TB (Figure 6.3-1) tracked together each year until 1986 when the SD colony suffered a large decrease in survivorship, while the TB colony took two years to approach a similar low value. In 1987, the SD colony survivorship improved, while the TB colony still decreased, and then, unfortunately, the TB colony was destroyed.

The first-year survivorship of *E. fuscus* cohorts also showed similar fluctuation at the two roost sites over the 12 years (Figure 6.3-1). There were noticeable extremes in 1988, for example, when the SD cohort had one of the highest survival rates of any cohorts at SD, while during the same year the TM-TB cohort dropped to one of its lowest values of survivorship.

In both of the intraspecific comparisons described above, the colonies at different roost sites appeared to be under similar pressures, since the colonies of the same species tracked each other with similar trends. However, when the two different species at the same roosts were graphed together (Figure 6.3-2) there were major differences in patterns of increasing and decreasing survivorship, and in the magnitude of those changes. The obvious question then becomes--what processes

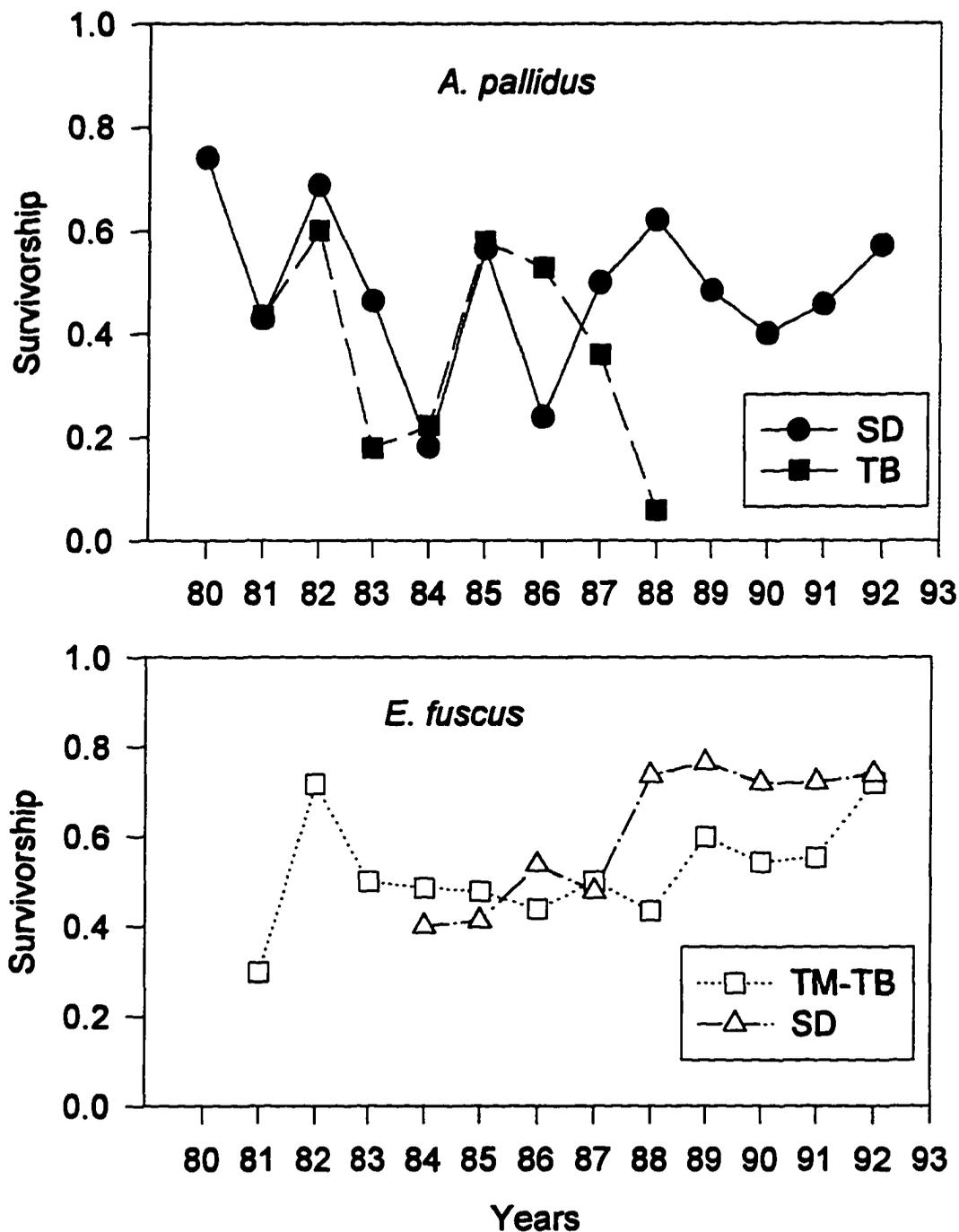


Figure 6.3-1. Intraspecific comparisons of first-year survivorship from individual known-age cohorts of *A. pallidus* and *E. fuscus* between roosts, 1980-1993. Sample sizes are listed in the life tables in Appendix B.

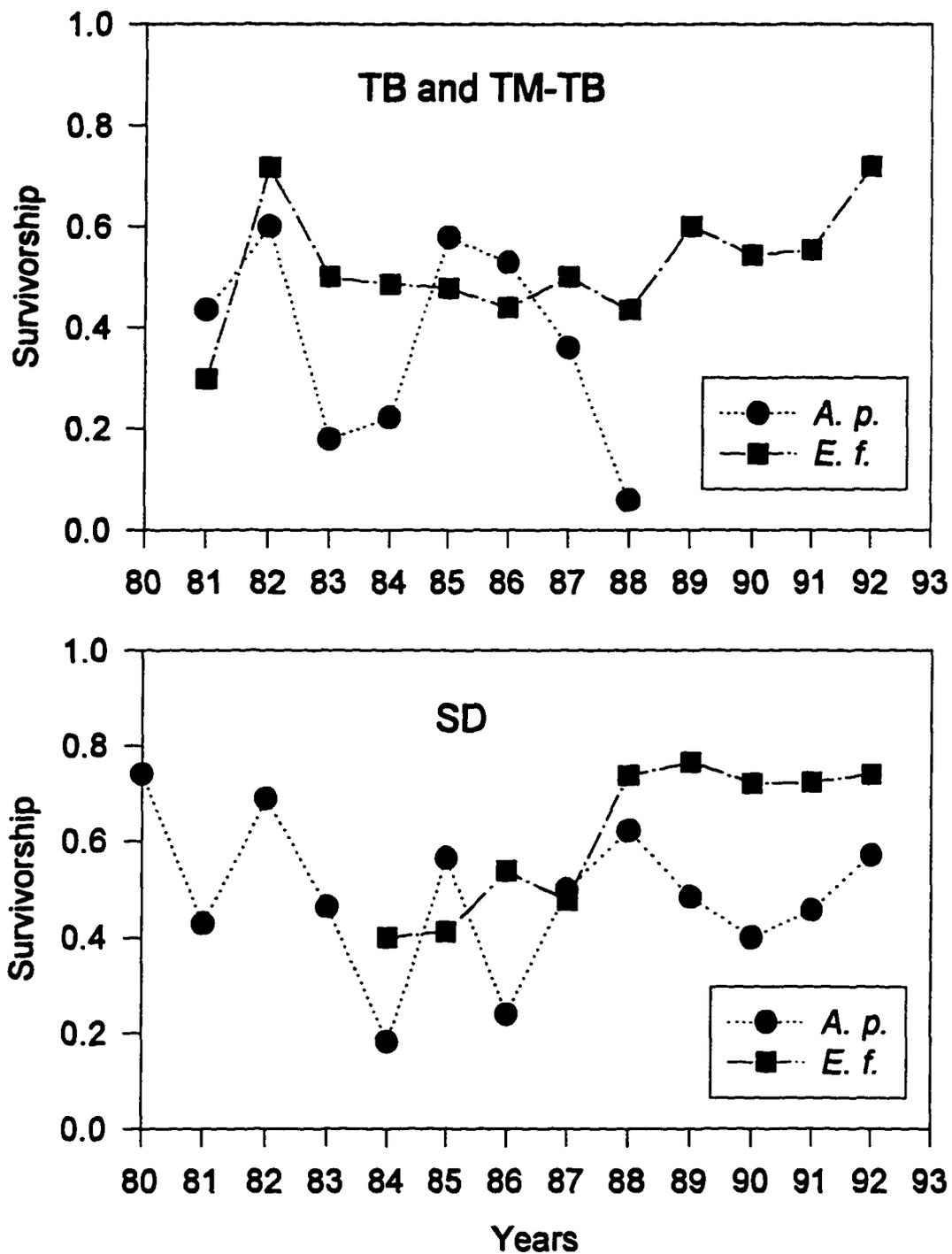


Figure 6.3-2. Interspecific comparison of first-year survivorship by roost, 1980-1993. Sample sizes are listed in life tables in Appendix B.

produced these patterns of survivorship of juveniles? Analyses of several possible factors that could influence first-year survivorship are presented below.

### 6.31 Roosts

Within species at the different roosts, first-year survivorship of *A. pallidus* varied from 1-29%, and mortality was higher at SD than at TB in four of seven year (Appendix B). Because there was no difference in survivorship for *E. fuscus* between TB and TM (when all juveniles in the study were combined; Table 6.31-1), and because some *E. fuscus* moved between these roosts, they were combined for analysis as the TM-TB colony. Mortality rates were higher at TM-TB than at SD in six of nine years for *E. fuscus* and varied from 2-30% between roosts during the same years (Appendix B). Four years of greatest intraspecific variation in mortality between roosts were not the same years for both species. Between species at the same roosts, *A. pallidus* had higher mortality rates than *E. fuscus* in seven of nine years at SD and four of seven years at TB (Appendix B). The years of highest interspecific variation in mortality were not the same at both roosts.

Comparison of the total numbers of juveniles (for years 1980 through 1992) for both species born at each roost site with the total number that survived to age one, showed significantly higher survivorship for both species at SD (Table 6.31-1).

Such differences in roost-specific survivorship seem most likely to result from differences in the rate or onset of development of young and/or from differences in

Table 6.31-1. Comparison of first-year survivorship at the different roosts. Juveniles from all cohorts are combined. There was no difference in percentage survival of *E. fuscus* between TM and TB, so numbers from these roosts were combined. Asterisks indicate significant chi-square tests (at  $P < 0.05$ ) that reject the null hypothesis of no difference in survival between roosts.

Species and Roost	% Surviving	Did not Survive	Survived	n	$\chi^2$ , 2 d.f.	P
<i>A. pallidus</i>						
TB	37	110	65			
SD	47	201	175			
				551	3.92*	0.048
<i>E. fuscus</i>						
TM	53	266	297			
TB	54	106	123			
TM&TB	53	372	420			
SD	63	78	135			
				1005	6.86*	0.009

the quality of the individual roost sites or their surroundings. In both cases, the result should be the presence of young at certain roosts that are larger in body size than are those at the other roost sites on the same date.

An example of differences in body size of young at the two roosts on similar dates was observed in 1982. Juvenile *A. pallidus* at SD on 18 August had significantly larger forearm and body mass measurements than the juveniles at TB on 20 August (part I in Table 6.31-2).

Of the *A. pallidus* juveniles at SD on 18 August 1982, those that survived to 1983 had significantly longer forearms than those who did not (part II in Table 6.31-2). Similar evidence was found for *E. fuscus* at the TM roost site. On 17 September 1983, a sample of juveniles who survived to the Spring of 1984 had significantly heavier body mass (but not longer forearms) than juveniles who did not survive (part III in Table 6.31-2). The fact that by mid-September, there were differences in mass but not forearm length for *E. fuscus* in this study is explained by the fact that forearm measurements of juveniles reach permanent adult length before the summer ends, while body mass does not reach adult levels until the following year; this variation in growth and development of juveniles also was reported previously for *A. pallidus* (R. Davis, 1969b).

To test the hypothesis that the larger-bodied young that occurred at the SD roost might be the result of earlier development due to earlier birth dates, the

Table 6.31-2. Juvenile size, roosts, and survivorship. I.) Size comparison of juvenile *A. pallidus* between roost sites on similar dates in 1982 (18 August at SD, 20 August at TB). II.) Comparison of forearm measurements for juvenile *A. pallidus* at SD on 18 August 1982 with first-year survivorship. III.) Comparison of body mass of juvenile *E. fuscus* at TM on 17 September 1983 with first-year survivorship. Forearm (FA) measurements in mm; mass in g. Asterisks indicate significant statistical test results at  $P < 0.05$ .

	Roost or Outcome	Trait	n	Mean	SE	Statistics
<i>A. pallidus</i>						
I.	SD	FA	32	54.5	0.252	$t = 6.23^*$ $P < 0.0001$
	TB	FA	27	52.1	0.309	
	SD	Mass	31	16.9	0.18	$t = 3.37^*$ $P = 0.001$
	TB	Mass	27	15.9	0.224	
<i>A. pallidus</i>						
II.	SD: survived	FA	23	54.9	0.296	$t = 2.37^*$ $P = 0.025$
	SD: did not survive	FA	9	53.7	0.343	
<i>E. fuscus</i>						
III.	TM: survived	Mass	24	18.9	0.551	$t = 2.07^*$ $P = 0.0485$
	TM: did not survive	Mass	5	15.9	1.709	

proportions of lactating females (and/or those giving birth) to the total number of female bats present were compared at each site to determine the relative timing of parturition. The results were inconclusive (Table 6.31-3) and did not provide consistent evidence of earlier parturition at the SD roost for either species. In fact, both *A. pallidus* and *E. fuscus* colonies at the SD roost seemed to have later periods of parturition (except for *E. fuscus* during 1989) than the TB colony or TM colony (for *E. fuscus*) during the years for which samples could be used to determine onset of parturition. In consequence, if young bats were consistently larger at the SD roost, then either there was a developmental advantage in later pregnancy and birth (perhaps because of roost temperatures that were undoubtedly higher at later dates), or the more optimal characteristics of the SD roost site allowed faster rates of development that more than compensated for later pregnancy and birth. No data are presently available to adequately test either of these aspects of roost site quality.

Roosts are presumed to be one of the most limiting factors in the distribution of bats (Humphrey, 1975). The benefits of roosts are diverse, and vary with the type of structure. For crevice-dwelling bats in temperate regions, the roost used for maternity function is especially important for providing optimal temperatures during pregnancy, lactation, and postnatal growth of young (Kunz, 1982), and in providing protection from predators directly or indirectly, when distances from the roost to

Table 6.31-3. Comparisons of the relative onset of parturition periods for I.) *A. pallidus* and II.) *E. fuscus*. The dates that are given are those available (colonies could not be visited continuously because of disturbance to parturient females) that were selected to provide comparable samples at each roost. "%PP" is the percentage of females present that were either post-partum or in the process of parturition on that date. "n" is the total number of adult females that were pregnant, parturient, or lactating. Onset "1 or 2" are rankings that indicate which colony had the earliest and second earliest dates of onset of parturition; this can be determined when the sampled date was later and had a lower %PP (2), or the sample had an earlier date and a higher %PP (1); exception, when dates were one day apart and the later date had a much higher %PP, it was considered (1). "X" indicates that ranking the onset of parturition was not possible (when %PP was higher on a later date, determination of onset was inconclusive). ">>" means onset of parturition was later than.

Year	TM colony	TB colony	SD colony	Conclusion
Date (n) %PP - Onset rank				
Ap I) 1984	---	19 June (36) 47%	21 June (50) 74%-X	---
1985	---	23 June (26) 92%-1	22 June (44) 66%-2	SD >> TB
1986	---	18 June (27) 96%-1	19 June (47) 85%-2	SD >> TB
1987	---	29 June (27) 78%-X	28 June (34) 62%	---
1988	---	22 June (27) 22%-X	21 June (42) 14%	---
Ef II) 1985	8 July (108) 75%-1	12 July (48) 63%-3	9 July (43) 63%-2	SD >> TM
1986	5 July (104) 77%-1	---	9 July (44) 68%-2	SD >> TM
1987	14 July (82) 95%-1	10 July (60) 60%-X	15 July (41) 76%-2	SD >> TM
1988	9 July (108) 68%	10 July (50) 70%-X	---	---
1989	9 July (96) 72%-3	5 July (56) 80%-1	8 July (58) 84%-2	TM >> SD

foraging sites are considered (Tuttle and Stevenson, 1982). Because the roosts in the present study were manmade structures, human presence was a potential influence on survivorship of bats using them (see Sec. 6.34).

### 6.32 Weather

The most obvious environmental factors that could affect survivorship of any population are the ambient temperature and rainfall patterns in the area where the animals occur. For example, in the present study, survivorship values for both species were extremely low in 1984 (Figures 6.3-1 and 6.11-2), and in 1984 total summer precipitation was at a 12-year high in that area. In consequence, I analyzed some measures of weather and tried to find correlations with the variation in first-year survivorship of bats at the Tombstone maternity roosts. The three roost sites are within 12 km of the station at Tombstone reporting to the National Oceanic and Atmospheric Administration, so I obtained weather data from the Arizona annual summaries for that station.

I broke the annual cycle into six month periods of "summer" when precipitation directly affects the bat colonies during their residence at the Tombstone roosts, and "winter" when it indirectly affects bats during their winter absence through its effects on the vegetation upon which insects must rely. I summed the accumulated monthly precipitation from May through October to give the "summer total precipitation" (STP) and summed the accumulation from November and December of that year with January through April of the next calendar year to yield the "winter total precipitation" (WTP) (Figure 6.32-1). I averaged the mean monthly

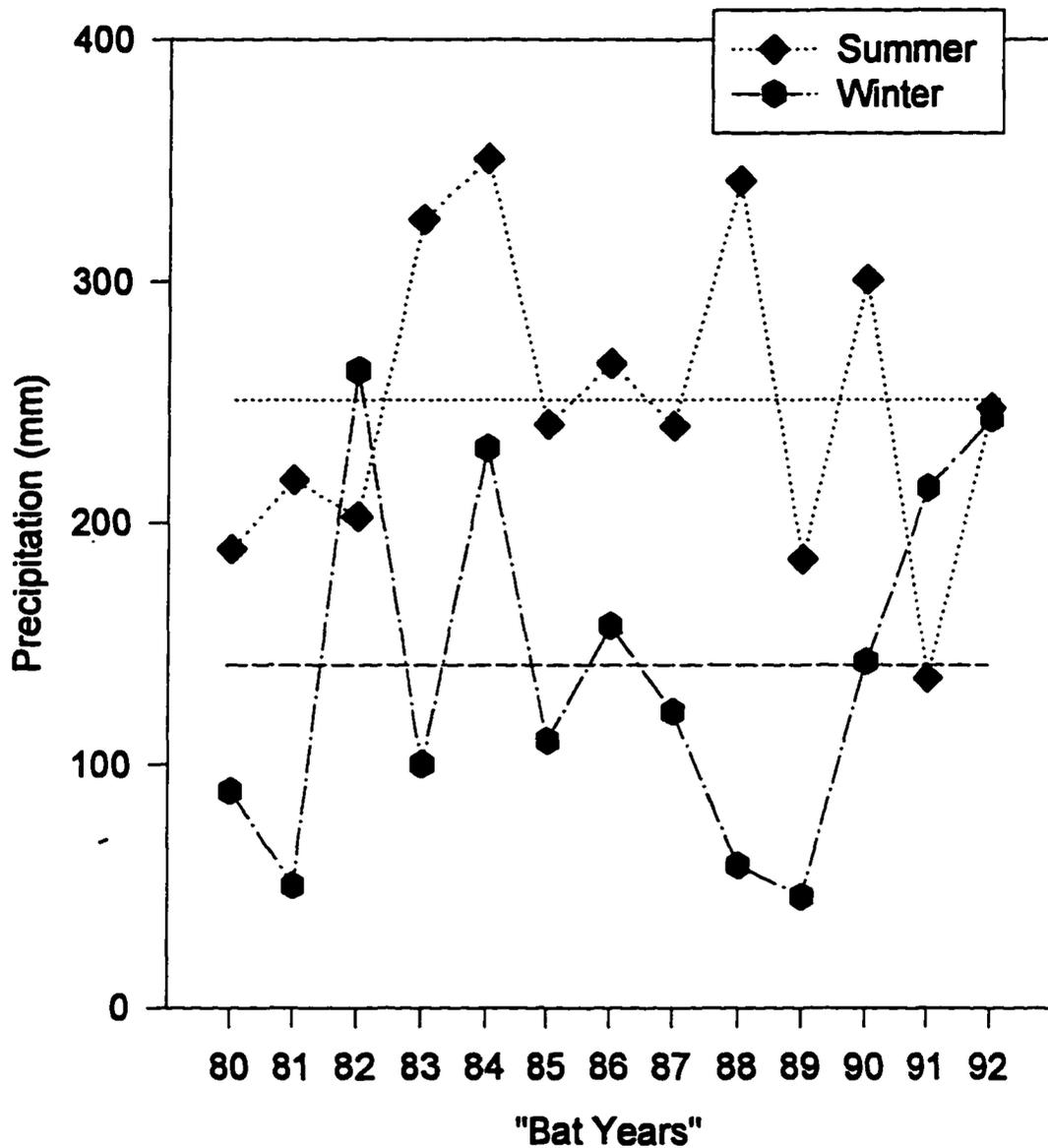


Figure 6.32-1. Total accumulated summer and winter precipitation at Tombstone. Monthly accumulated precipitation is taken from NOAA records. A "bat year" begins in summer (May through October) and ends after winter (November through April). Long dot and dash lines are 12-year means.

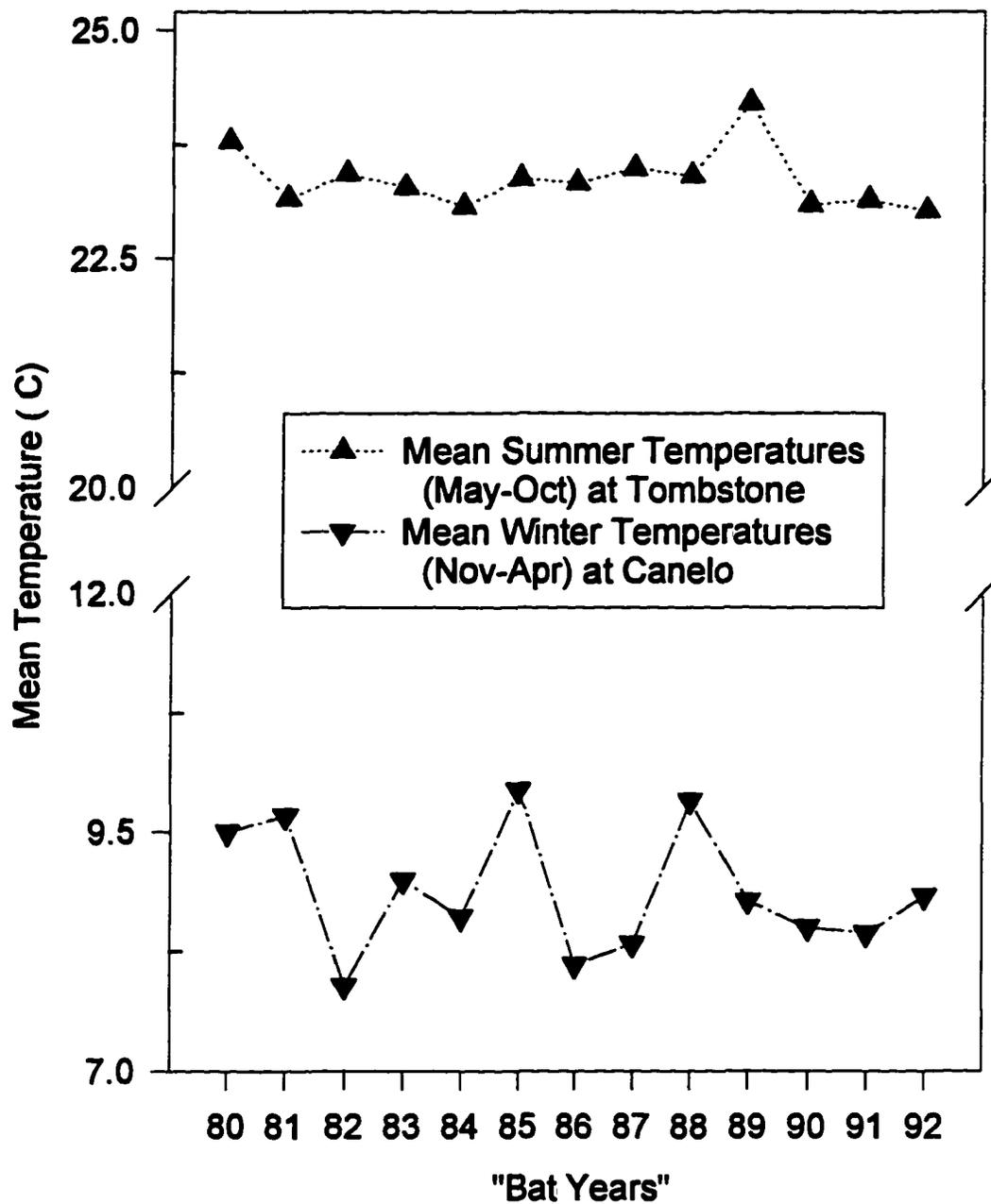


Figure 6.32-2. Annual average-of-the-means of summer and winter temperatures at Tombstone and Canelo stations. Data are from NOAA records.

summer temperatures for the six-month summer period to produce the "summer average temperature" (SAT) for each "bat year" of the study (Figure 6.32-2). I selected the Canelo weather station for the temperature records during the winter period (Figure 6.32-2), November through April, when bats are not permanently in residence at the maternity roosts and are assumed to be in hibernation at elevations comparable to Canelo. Canelo was selected somewhat arbitrarily as a winter-locality surrogate, since the actual whereabouts of the bats are not known during this period. There were only two off-site recoveries of any of the bats from the roosts in the present study. Both were *E. fuscus*; one was from the city of Sierra Vista at the base of the Huachuca Mountains, and the other was from a canyon in the Huachucas (see Sec. 6.33). No continuous weather data are available for either of these localities. Canelo is located at 1528 m elevation, at the base of the Huachuca Mountains in open Madrean Evergreen Woodlands habitat. I averaged the monthly temperatures for the "winter" period to yield the "winter average temperature" (WAT) for each bat year of the study (Figure 6.32-2). I entered these weather factors as independent variables into a forward stepwise multiple regression with first-year survivorship as the dependent variable.

*Antrozous pallidus*.— Summer precipitation, the first variable selected into the stepwise regression, was the only climatic variable that had a significant coefficient ( $-0.0014$ ,  $t = -2.65$ ,  $P = 0.016$ ; Figure 6.32-3). This regression model described a

significant inverse effect of summer precipitation on survivorship ( $r = 0.530$ ,  $d.f. = 19$ ,  $F = 7.05$ ), but explained only a relatively small proportion of the variability in survivorship ( $r^2 = 0.281$ ), and the power of the test was low (alpha = 0.05: 0.683). This low  $r^2$  value is not surprising since the inverse effect of summer rainfall could only influence the summer half of first-year survivorship.

Hoping to explain more of the variation in survivorship, I entered the four climatic variables into a multiple linear regression. The resulting model was significant ( $r = 0.687$ ,  $d.f. = 19$ ,  $F = 3.35$ ,  $P = 0.038$ ); more of the variation in survivorship was explained ( $r^2 = 0.471$ ), and the power of the test was high (alpha = 0.05: 0.935), but none of the climatic variables was then significant. At least two of the variables, WTP and WAT, were co-correlated ( $n = 20$ ,  $r = -0.675$ ,  $P = 0.001$ ), but removing one or the other did not increase the value of  $r^2$ , and produced a regression model that was not significant.

I tried a simpler two-variable model using only STP and WAT as the independent variables. This model described a significant effect of these two variables on first-year survivorship ( $r = 0.584$ ,  $d.f. = 19$ ,  $F = 4.40$ ,  $P = 0.029$ ). In particular, STP had a statistically significant coefficient ( $-0.0014$ ,  $t = -2.785$ ,  $P = 0.0137$ ) and while WAT did not have a significant regression coefficient ( $0.057$ ,  $t = 1.244$ ,  $P = 0.230$ ), the significant influence of both variables explained 34% of the variability. The decrease in power of this test (alpha = 0.05: 0.788) however,

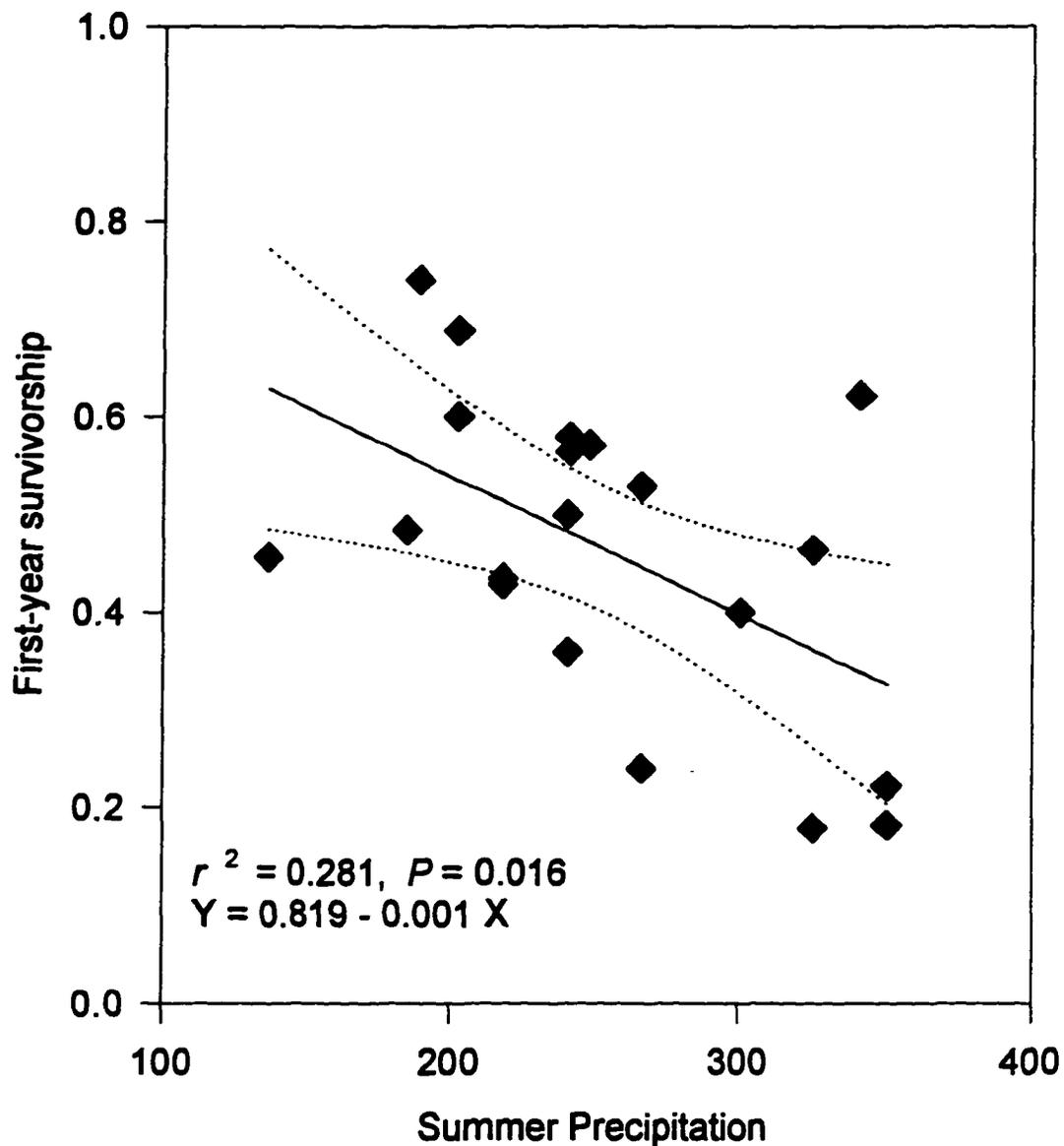


Figure 6.32-3. Effect of total accumulated summer precipitation on first-year survivorship of *A. pallidus* at SD and TB, 1980-1993. Weather data are from NOAA records. Dotted curves are 95% confidence intervals.

suggested, not surprisingly, that there is much more to be learned about the relationship of weather on survivorship.

*Eptesicus fuscus*.-- None of the independent variables about weather, individually or in any combination, showed a significant influence on survivorship in forward stepwise regression. This, of course, does not mean that weather was not a factor in the survivorship of *E. fuscus*. Rather, it suggests that the effects may be complicated, and that there are undoubtedly other factors that play important roles in influencing survivorship.

*Discussion*.-- Differences in the effects of weather on the two species may be due in part to the timing of parturition. Weather has been shown to be an important factor affecting population levels of *Rhinolophus ferrumequinum* in Great Britain where numbers declined after years of cold spring and summer weather, and these unfavorable weather conditions were correlated with later timing of birth (Ransome and McOwat, 1994).

The period over which parturition took place for colonies of *A. pallidus* at the Tombstone roosts was earlier than for *E. fuscus* (Table 6.31-3). During the present study, parturition was found to occur from the second week through the end of June for *A. pallidus*, verifying the mid-June parturition dates originally reported (R. Davis, 1969b). I only found three *A. pallidus* pregnant in July (surprisingly, one of these was still heavily pregnant on 15 July; this unusually late birth involved a five-

year old female and apparently was not harmful to her, because she lived to be 9 years old). In this study, parturition for *E. fuscus* usually occurred during the last week of June and the first two weeks of July (with many examples of females still being pregnant as late as 15 July).

In North America, later parturition occurs in populations of *E. fuscus* at increasingly northern latitudes, and this difference in reproductive timing is thought to be due to temperature differences (Kunz, 1974).

The timing of parturition for populations of *E. fuscus* from different geographical locations in North America has received much attention. In Maryland, parturition apparently occurs during the latter half of May and first half of June (Christian, 1953); in Kentucky, most young are born during the last week in May and the first week in June (Barbour and Davis, 1969); in central Kansas, parturition begins in late May and extends into the second week of June (Kunz, 1974); in Iowa, it is nearly two weeks later, mostly in late June (Kunz, 1971); in North Dakota, parturition probably occurs from late June to early July (Jones and Genoway, 1966 in Kunz, 1974); in northwestern Texas, some females have been observed to have given birth on 31 May (Jones and Manning, 1990); in southern California, births occur in the latter part of May and early June (Barbour and Davis, 1969); in New Mexico, parturition begins during the last week in June with pregnant females noted through 12 July (Findley et al., 1975); in Wyoming, pregnant females have been observed as

late as July (Clark and Stromberg, 1987); in Oregon, pregnant females have been captured on 26 June (Bailey, 1936 in Christian, 1953); in Alberta, most young may be born in the latter part of June with first parturition as early as 5 June and pregnant females still observed on 12 July (Schowalter and Gunson, 1979). These examples show a general trend toward later dates of parturition at more northern latitudes, probably because insect availability would increase later in the summer with warmer environmental temperatures (Kunz, 1974). This hypothesis would predict that *E. fuscus* in southeastern Arizona should have early parturition dates, i.e., in May or early June, because of the southern latitude. However, as is true for dates of parturition in New Mexico, in the present study, both species of bats had relatively later dates than would be expected on the basis of latitude.

In southern Arizona, selection for delayed parturition would not be the result of waiting for the warmth of summer as is probably the situation in more northern latitudes. Rather, in Arizona's portion of the Chihuahuan desert, May and June are the harshest period of Spring and Summer, when the climate is extremely dry and hot. In contrast, the end of June and beginning of July bring summer rains that probably translate into an abundance of insect prey, and thus, the shift toward later dates of parturition. However, the balance must be towards timing it so that young bats are not ill-affected by summer storms.

Bats living in the Chihuahuan desert in the summertime must cope with a dry warm period during May and June, followed by a wet period in July, August, and September. Bats roosting in a bridge expansion joint face environmental temperatures that affect crevice temperature, depending upon how the structure blocks the radiant energy of the sun, the way the substrate accumulates and loses heat, and the way in which cooling occurs as cold air drainage in the wash moves along under the bridge. The bridge structure serves to protect the bats from the direct effects of rainfall, but when rain occurs, undetermined amounts of water typically accumulate on the road surface and drain down onto the bats in some of the expansion joint crevices. Temperatures within a roost are a combination of the external environment and the temperature of the bats themselves, in clustered union, or individually (Kunz, 1982). For bats out of the roost, generally at night, the environmental temperatures pose other considerations. The cooler temperatures at nightfall affect feeding activities and promote such behaviors as night roosting in places external to the day roost.

In the Sonoran desert near Tucson, both a shift in the rainfall pattern and an increase in the amount of total annual rain have been shown to cause dramatic increases in the production of seeds and growth of vegetation, and to result in spectacular increases in the size of rodent populations (Petryszyn, 1981). Thus I expected that in the Arizona portion of the Chihuahuan desert, years (or seasons) with high total rainfall might have a positive effect on growth of vegetation, a

corresponding indirect influence on the insect populations on which these two species of bats feed, and perhaps a resulting positive effect on first year survivorship of bats. What was unexpected was the negative relationship of rainfall and survivorship (Figure 6.32-2) which at first seemed nonintuitive. However, the negative effect of total summer precipitation on juvenile *A. pallidus* survivorship can be rationalized considering the kind of summer storms that occur in the Arizona portion of the Chihuahuan desert, with sudden heavy rainfall, rapid cooling temperatures, and high winds, and the fact that inexperienced juvenile bats must fly and feed during such periods of severe climatic activity.

I witnessed some flash floods passing under these bridge roosts. Such floods would be catastrophic for young bats that fell out of the crevice roosts or got washed out when water poured through the expansion joint from the highway above. Two juvenile *A. pallidus* that I found out of the roost in July 1992, appeared to be examples of the problems that summer rains pose for juvenile bats. One was dead on the ground below the roost. It was mud-covered and had its feet tightly encased in hardened balls of dried mud as if it had been trying to crawl and only managed to make "mudballs" within its toenails. The ground all around the bridge was covered by dense slick mud, and there was a fresh deep cut in the bank that extended from the road surface down into the wash, a sign of recent heavy rainfall and extensive runoff from the asphalt roadway. The other juvenile was found lying on the bridge span

beneath the cluster of hanging bats. This bat also had dried balls of mud clogging its toenails such that it could not possibly use its toenails to climb back up into the roost or to hang there in the normal manner. This bat was emaciated and near death, and because it was not in the crevice with the others, it was subjected to cooler temperatures and moisture in the mud upon which it rested. A week later at this same roost, I found a juvenile *E. fuscus* lying on the ground beneath the bridge in a similar mud-clogged condition. The perils of summer rains affect both species (although perhaps not to the same extent).

If it is not the difference in timing of parturition between the two species, I cannot explain why the summer precipitation that was found to have a significant inverse effect upon survivorship of *A. pallidus* (Figure 6.32-2), did not also show an equivalent effect on the survivorship of *E. fuscus*. Clearly, both species are adversely affected by floods, water draining into their roosts, mud, high winds and heavy rain. However, the two species differ in methods of foraging (see Sec. 4.1 above), and they may differ correspondingly in certain aerodynamic characteristics. Such differences would explain a lessened negative impact of summer rainstorms on *E. fuscus*.

### 6.33 Nonhuman biotic factors

Biotic factors reported to produce mortality in bats, including ectoparasites, diseases, and various predators (Allen, 1939; Tuttle and Stevenson, 1982), were observed directly during the present study, or were inferred to be affecting juvenile survivorship.

*Ectoparasites.*— Mites, ticks, nycteribiids (bat flies), and cimicids (bedbugs) that are commonly associated with bats (Whitaker, 1988) were collected from *A. pallidus* at both roosts. Mites and cimicids were also observed on *E. fuscus* at all roosts. Numbers of *Cimex* sp. (bedbugs) on the walls of the roosts appeared to increase during the maternity season. These parasites were observed only infrequently on bats of either genus, but when present were found especially on the elbows and forearms of young bats. No attempts were made to quantify the ectoparasite loads on these colonies, but their numbers appeared to be highest on walls near where *E. fuscus* most often roosted. Colonies of *A. pallidus* that were studied in Oregon were found to switch roost sites extremely often, despite the potentially high costs of doing so, and this behavior was correlated with high ectoparasite loads (Lewis, 1996). However, neither *A. pallidus* or *E. fuscus* changed roost sites frequently during the current study, and certainly not to the extent that was observed in Oregon, thus, ectoparasite loads at the Tombstone roosts were either not as problematic, or this was

not an important criterion for roost site selection, or there were no alternate roost sites that were suitable.

*Disease.*— Rabies infection has been documented in every species of insect-feeding bat in the U.S., including *A. pallidus* and *E. fuscus* (Brass, 1994); however, the infection rate of rabies in samples of bats that are asymptomatic for rabies is less than 0.5% (Constantine, 1988), so rabies possibly, but not very probably, plays a role in survivorship in these colonies. Rabies was the suspected cause of unusual behavior that I observed only once in 1983 at the TB roost when an adult female *A. pallidus* went into convulsions that lasted more than a minute before she died. This bat tested negative for rabies (Pima County Health Department). The cause of the convulsions was unknown.

However, an example from 1985, in which an *E. fuscus* that appeared to be normal (except that it was still present at TM on 4 October—a relatively late date for *E. fuscus* to be present at the maternity roosts) demonstrated the fact that rabies does occur in these colonies. I was informed by an acquaintance who had kept this full-grown juvenile female in captivity that the bat was maintained alone, kept on a healthy diet (Wilson, 1988), and given flight exercise and other attention frequently. The bat was docile and responded well to feeding and handling, and continued to appear to be healthy. During April 1986, six months after its confinement, the bat became irritable, then lethargic, and died. It tested positive for rabies (Pima Country

Health Department). The mother of this bat, a four year-old at the TM roost in 1985, did not ever return. It is possible that the mother also was ill.

The incubation period for rabies in bats is variable. Experimentally-infected bats have lived as long as six month after infection (Constantine, 1970). Bats infected naturally before being brought into captivity usually died within three months, although a rabid *E. fuscus* died 209 days after capture (Constantine, 1988), and more than a year's incubation has been reported for a bat (Brass, 1994).

*Predation.*-- At least seven species of vertebrates that previously had been reported to be predators of bats (Tuttle and Stevenson, 1982) were observed in, or near the bridge roosts in the present study. These included great-horned owls, kestrels, roadrunners, a coachwhip snake, and gopher snakes, all of which were observed within a few meters of the roost crevices. Although it is unlikely that any of these predators could remove a bat from a bridge crevice, they certainly could capture fallen bats, or (in the case of owls or hawks) bats that had left the expansion joint roosts during foraging flights. Of these potential predators, I saw a kestrel chase a flying *A. pallidus*, and I watched a roadrunner grab in its bill a juvenile *E. fuscus* that I had released to test its age-specific flight ability. I found a *Neotoma albigula* in the TB roost crevice a few times, and I repeatedly observed *Peromyscus boylii* in the crevices at all sites. Both of these rodents are unlikely predators on adult bats, but they could certainly eat a new born young.

In 1989, a regurgitation pellet that had been deposited during the period 7-24 February by a Mexican spotted owl, *Strix occidentalis lucida*, was found to contain *Eptesicus* bones and an aluminum band from an *E. fuscus* that I had banded as a juvenile male at the TB roost (44 km away) in July 1988. Besides evidence of predation, this recovery suggested the possibility of a winter hibernaculum of these bats in the Huachuca Mountains. In southern Arizona, of 11 species of insectivorous bats reported from pellets of spotted owls, the most frequently occurring bats were *E. fuscus* and *A. pallidus* (Duncan and Sidner, 1990).

Some authors have suggested that owls are a major source of mortality to bats (Tuttle and Stevenson, 1982). However, unless the owls are actually roosting in the same structure with the bats (as is often true of barn owls), others have shown that despite large diversity of bat species in owl pellets, bats actually make up a very small percentage of prey items of most species of owls (Duncan and Sidner, 1990).

#### 6.34 Human disturbance

Disturbance at these roosts was evident in various ways, from carcasses containing BB pellets to skeletons encrusted in road tar within the expansion joints. Whether human disturbance was intentional or not, it had the same deadly consequences.

*Vandalism.*— Litter left on the ground or even on the bridge supports provided evidence of visitations to these roost sites, by other people during my 15 year study.

On at least seven occasions that I witnessed, other people approached the underside of the bridges, and eventually spoke with me and told me that they knew the bats were present; and on a few other of my visits, highway construction crews walked under to question me about the bats. In 1983, I intercepted another researcher at the SD roost in the process of capturing *A. pallidus* that I had banded. He had caused compound fractures to the humerus or radius of at least three of the 23 bats he had collected. Although *A. pallidus* recovers naturally from breaks to the phalanges (R. Davis, 1968), they do not survive breaks to the major arm bones without being artificially maintained in captivity (Sidner and Davis, 1986).

I discovered three other episodes of human disturbance that caused more substantial mortality to these colonies. In 1989, only five *A. pallidus* were found alive at the TB roost. The bodies of these bats, and the carcasses of two *A. pallidus* and two *E. fuscus* that had recently died, offered evidence that the bats had been trapped in the crevice when the road above was tarred, and hot liquid tar had flowed down through the expansion joint into the roost crevices. A state worker confirmed that several days earlier the Arizona Department of Transportation had performed this work despite his protest that there were bats inside and that he knew someone was studying them. The bats that were still alive had lost their fur and the exposed skin of their bodies was reddened as if burned; they were emaciated, dehydrated, and their wings were partially tarred closed so that flight was impossible. Four of the bats were

lactating but their young were not present, and one female was heavily pregnant. I removed the tar from their wings and bodies, and provided water and food. In data analysis, I treated these as dead bats, because I am certain they could not have survived without my intervention. In 1987, the colony of *A. pallidus* at TB had numbered 30 adult females, 25 juvenile females, and 18 juvenile males; and in 1988 it contained 27 adult females, 18 juvenile females and 19 juvenile males (Table 6-1). In 1989, the colony was essentially no longer in existence.

The extreme fidelity of *Antrozous* to these maternity roosts (where they were either born or where they had given birth previously and raised young) was demonstrated by the return to TB in 1990 of three of the rehabilitated adults from the tarring episode. During the summer of 1990, each raised two young. In 1991 and 1992, two of the rehabilitated adults (now aged four and five years old) and one of their daughters returned and raised young. In 1993, none of the tarred bats returned, although the daughter and two subsequent female offspring did. However, in 1994 and 1995, no *A. pallidus* were observed at the TB roost.

The second major incident occurred in 1990, 10 days after the first portion of the colony of *E. fuscus* at the TB roost had been banded. I returned to find a total of 16 dead or dying juveniles, three dead adult females, and there were missing adult females who should have been present since their banded young were present. The dead and injured bats had broken bones, holes in their flight membranes, and two

bodies had BB shot lodged in their flesh. Witnesses described two preteen boys from a nearby trailer park who had been shooting birds, and these children, when confronted by me, admitted to having used a BB gun to shoot at the colony. The size of the *E. fuscus* colony there in 1989 was 59 adult females, and in 1990 there were 63 adult females, but in 1991, the year after the BB-gun episode, the colony numbered only 49 adult females (Table 6-1).

During one visit in 1994, I found 10 dead adult female and 24 dead juvenile *E. fuscus*, 2 dead juvenile *A. pallidus*, and 2 dead adult *Tadarida brasiliensis* on the ground and beneath the roost on the bridge supports at the SD roost. This third episode of human-caused mortality had occurred recently, probably within the last 48 hours, and there were wads from fired shotgun shells among the carcasses and on the bridge supports. The colony of *E. fuscus* at SD that had numbered 116 adult females in 1993, consisted only of 74 and 77 adult females in 1994 and 1995 following this shotgun episode (Table 6-1).

These three events that caused significant mortality are the ones that I happened to discover; it is possible that other such events occurred but were undetected. For example, the colonies of adult females at the various roosts have in some years shown unexplained decreases in population size that are similar to those described here for human-caused mortality in 1989 at TM and in 1994 (Table 6-1).

These colonies of bats are using artificial roosts, and because of their accessibility to humans, there may be serious potential risk to bats using them. On the other hand, if roosts are the limiting factor to bat distribution and abundance (Humphrey, 1975), then even these potentially dangerous sites may offer any of several benefits that outweigh the cost imposed by humans. For example, roosts located along relatively mesic desert washes may provide easy accessibility to foraging sites, although this may be of minor importance to bats, since insect-feeding bats appear to have very low energetic costs of transport that can be made up easily with energy assimilated from relatively few prey items (Fenton, 1997). It is more likely that these roosts offer optimal temperatures and better protection from the risk of predation or from the harshness of climatic conditions than natural roosts, at least during the maternity season. One can only hope that the strong site attachment of these bats to artificial roosts has not come as the result of the loss of natural roosts.

*This study.*— My presence at these maternity roosts must also have had a negative impact. This is true of any empirical study of wild animals in which the researcher directly handles or otherwise disturbs a population, and such disturbance would undoubtedly be most serious during the maternity season. However, to obtain age-specific data on life history features that involve known mother-young relationships, it is necessary to capture, mark, and recapture specific individuals during this critical period. The researcher has the responsibility to minimize negative

effects wherever possible, and I attempted to do so, but that does not negate any impact that I may have caused.

Estimates of negative consequences caused by researchers are rarely given. In earlier studies of survivorship (Table 4-1) there was evidence that the researchers themselves were responsible for the loss of some portion of the population (Mills et al., 1975; Tuttle and Stevenson, 1982), but the extent of this was limited to brief mention in the methods section about the season of year during which visits occurred, or the actual number of visits to the site, or the rate of visitation, for example, as weekly or monthly visits (R. Davis, 1969b; Kunz, 1974; Ransome, 1995). I attempted to estimate my disturbance to the first-year survivorship of these bats.

Earlier in this report, multiple linear regression was used to describe the potential effects of certain weather variables upon first-year survivorship for both species (see Sec. 6.32). I added another independent variable, the number of researcher work-visits (NOV) to the roosts of each species, into the multiple linear regression. For *A. pallidus*, when NOV was added with the climatic variables, summer total precipitation and winter average temperature, both STP and NOV had significant coefficients (STP:  $-0.001$ ,  $t = -2.137$ ,  $P = 0.048$ ; NOV:  $-0.019$ ,  $t = -2.511$ ,  $P = 0.0231$ ). This new model with a high value for the power of the test ( $\alpha = 0.05$ : 0.9669), described a significant negative effect of weather and

disturbance together on survivorship ( $r = 0.726$ ,  $d.f. = 19$ ,  $F = 5.95$ ,  $P = 0.006$ ), and explained more of the total variation in first-year survivorship ( $r^2 = 0.528$ ).

For *E. fuscus*, a significant regression model was not found using the climatic variables as independent variables against survivorship (see Sec. 6.32). However, when NOV was added with the three climatic variables, STP, WTP, and SAT, three of these variables showed significant coefficients (WTP: 0.001,  $t = 2.29$ ,  $P = 0.036$ ; SAT: 0.245,  $t = 2.163$ ,  $P = 0.046$ ; NOV: -0.021,  $t = -2.664$ ,  $P = 0.017$ ), and a modest amount of the variation in survivorship ( $r^2 = 0.462$ ) was explained and supported by the high power value power of the test ( $\alpha = 0.05$ : 0.940). (Results of the NOV independent variable against survivorship in simple linear regression is not given, because the regression failed a test for constant variance, Spearman rank correlation;  $P = 0.012$ ).

The negative impact of my visits has undoubtedly come from several sources, one of which was the necessity of using bands to uniquely identify bats. Concern about the banding of bats has been expressed in the bat literature from time to time, and there is evidence that bands may cause problems. Researchers must consider whether bands are necessary to achieve the objectives of their study. For studies such as this one, which involved age-specific survivorship, the individuals had to be permanently identified, so bands of the recommended size and type were used (Barclay and Bell, 1988). I filed smooth on each band any rough edges I felt against

my skin before placing them on a bat to decrease the likelihood of causing damage. Constantine (1967) noted that considerable pathology occurred to the relatively fleshy forearms of *Tadarida* when they were banded improperly. Such pathology was also observed in *A. pallidus* and *E. fuscus* during this study, although it was usually possible to detect and compensate for problems before they became serious (by adjusting, or by moving bands from one wrist to another). The problems that bands caused in both species were different degrees of abrasions to the wrists, and holes in the propatagia, plagiopatagia, and dactylopatagia, and infrequently trauma to the bones of the forearm. Judging by overall body condition and body mass, however, bats suffering from these problems typically appeared to be in as good general health as bats without such injuries (although judgments about health can be misleading; Barclay and Bell, 1988). In any case, while tissue damage can never be considered inconsequential, *A. pallidus* regularly suffer natural wing damage and appear to recover naturally and rapidly (R. Davis, 1968). An increased ability to overcome injury and infection quickly would be advantageous for bats because they fly on wings of living tissue (unlike the wings of birds).

In addition to bands causing wing damage to the bats, sometimes the bats also did damage to the bands. In such cases, if the damage had been caused by chewing, it is possible that a potential problem would result from increased tooth wear or an increase in wasteful time and energy (Barclay and Bell, 1988).

In the present study, these problems of wing or band damage were more numerous for *E. fuscus* than for *A. pallidus*. In fact, of 2231 banded *E. fuscus*, 324 bands needed to be replaced or moved, while 62 band changes were required for 1702 banded *A. pallidus*. Very few of these band changes were made on bats banded as prevalent juveniles, because juveniles apparently are more likely to accept bands than adults.

It is important to point out that the necessary disturbance resulting from my visits was similarly distributed between the two species. Thus, during this study, while I personally found my disturbance objectionable, it was like a controlled variable between the two groups; and in consequence, while it undoubtedly affected the empirical values, it should have played only a minimal role in influencing the comparative results.

#### 6.4 Factors involving maternal productivity

There are intrinsic influences, resulting from or dependent upon the survivorship and/or productivity of the mother, that may affect juvenile survivorship. For example, whether maternal age does or does not directly affect juvenile survivorship, maternal age can have an indirect influence if it affects the size of young; because bigger young of both *A. pallidus* and *E. fuscus* in this study had higher survivorship than smaller young (Sec. 6.31). But while maternal age has been shown to directly influence litter size in *A. pallidus* (R. Davis, 1969b), no determination has been made previously about the size of individual young with litter size. For *E. fuscus*, no information has been previously available about maternal age effects of any kind (Tuttle and Stevenson, 1982).

##### 6.41 Age of mother

If maternal behavior improves with experience and physical maturity, then it would be reasonable to expect that increased maternal age would reflect an increase in the probability of the survival of her offspring. This hypothesis was tested by comparing the number of young who survive to yearling age with the mothers' ages.

Within species, there were no significant differences in the proportion of young that survived versus the adult female age classes of the identified mothers of these juveniles during the first four years of maternal ages (Table 6.41-1). There were also no differences when maternal ages one and two years (the "least

Table 6.41-1. Juvenile survivorship and maternal age. Known-age cohorts of identified mothers of tested young were combined for different years. All chi-square values for tests of the null hypothesis that juvenile survivorship is independent of maternal age were less than the critical value ( $\chi^2 = 3.84$ ,  $P = 0.05$ ,  $d.f. = 2$ ) to reject the null hypothesis.

Maternal Age	n	Proportion Surviving	Statistics
<i>A. pallidus</i>			
1	70	0.471	Age 1 vs 2: $\chi^2 = 1.25$ , $P = 0.26$
2	89	0.371	
			Age 2 vs 3: $\chi^2 = 1.63$ , $P = 0.20$
			Age 1&2 vs 3&4: $\chi^2 = 0.96$ , $P = 0.33$
3	68	0.485	Age 4 vs older: $\chi^2 = 1.02$ , $P = 0.31$
4	46	0.458	
5	22	0.455	
6	16	0.250	
7	7	0.286	
8	1	0	
9	2	0.500	
<i>E. fuscus</i>			
1	44	0.500	Age 1 vs 2: $\chi^2 = 0.13$ , $P = 0.71$
2	89	0.551	
			Age 2 vs 3: $\chi^2 = 0.01$ , $P = 0.99$
			Age 1&2 vs 3&4: $\chi^2 = 0.01$ , $P = 0.99$
3	73	0.562	Age 4 vs older: $\chi^2 = 0.34$ , $P = 0.56$
4	47	0.511	
5	36	0.611	
6	20	0.550	
7	15	0.600	
8	12	0.500	
9	2	0.500	
10	3	0.667	

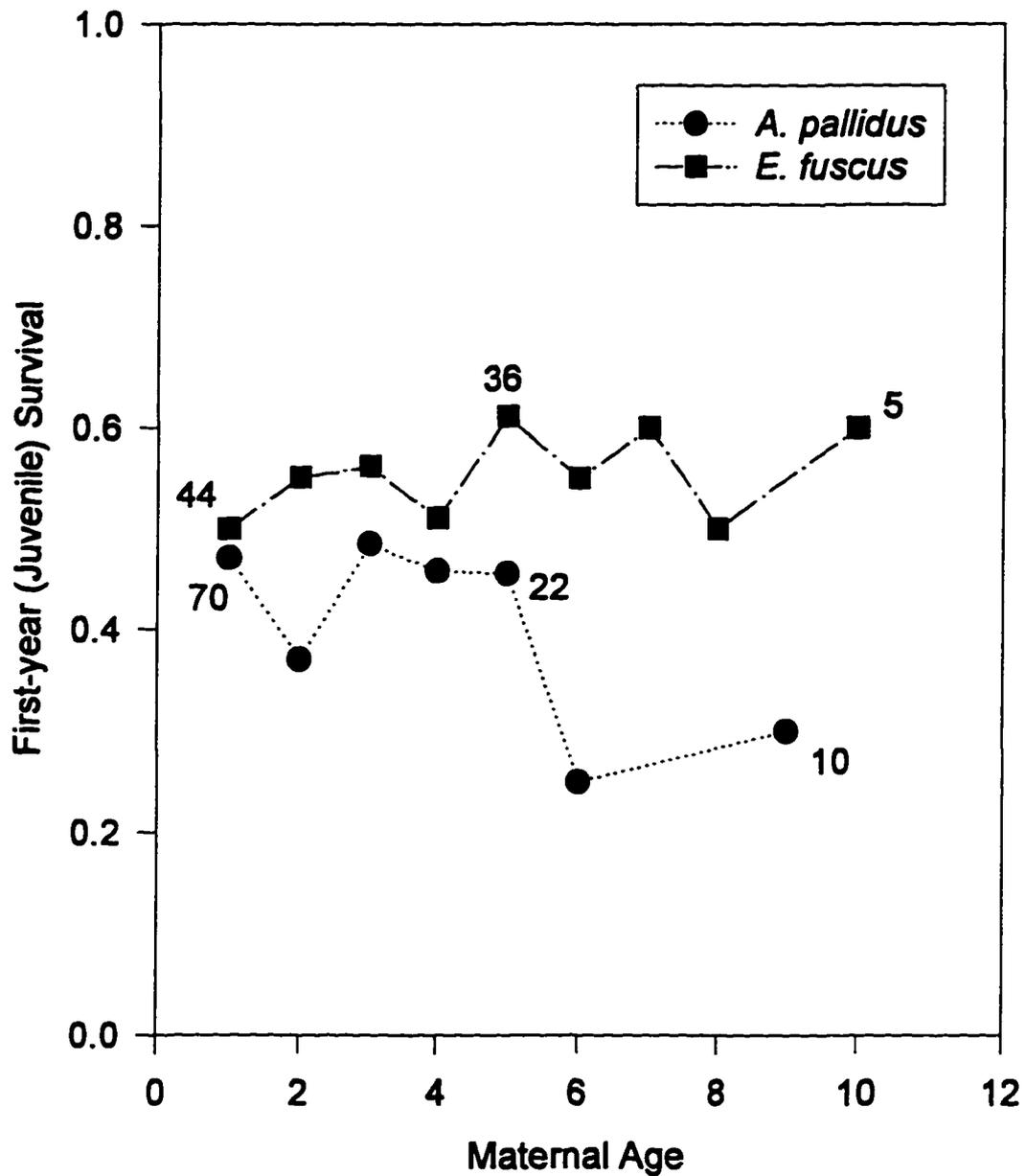


Figure 6.41-1. Comparison of juvenile survival with maternal age for *A. pallidus* and *E. fuscus*. The ages for which the sample sizes of the oldest mothers were very small were combined, so for *A. pallidus* age 9 is actually ages 7, 8, and 9 combined; for *E. fuscus* age 10 is actually ages 9 and 10 combined. Sample sizes for some of the points are indicated.

experienced age classes") were compared with older ages three and four. However, juvenile survivorship between the species was different; *E. fuscus* had higher rates of juvenile survival for every age of the mothers (Figure 6.41-1). The significance of the lack of a direct influence of maternal age on survival of young within species, as well as the differences between species, must both be considered in relationship to litter size.

#### 6.42 Percent twinning as a function of maternal age

Age-related variation in litter size was confirmed for *A. pallidus* and documented for the first time for *E. fuscus* in southeastern Arizona (Figure 6.42-1). The production of twins by older *A. pallidus* mothers that was originally reported (R. Davis, 1969b), was verified and now explained as a progressive maternal age-dependent change in litter size (Figure 6.42-1). The variation in litter size with maternal age was more pronounced in *A. pallidus*. The shift from one to two young per litter began at age two when 55% of *A. pallidus* mothers but only 9% of *E. fuscus* mothers had twins. At age three, the twinning rate had climbed to 70% for pallid bats and 23% for big brown bats. The steepness of the curve of age-dependent litter size decreased by age four when 78% of *A. pallidus* and 24% of *E. fuscus* mothers had twins. The proportion of twins produced at each age for both species continued to increase into old age. For *A. pallidus*, 100% of nine-year old females produced twins, but this may not be an accurate reflection of twin births at old age,

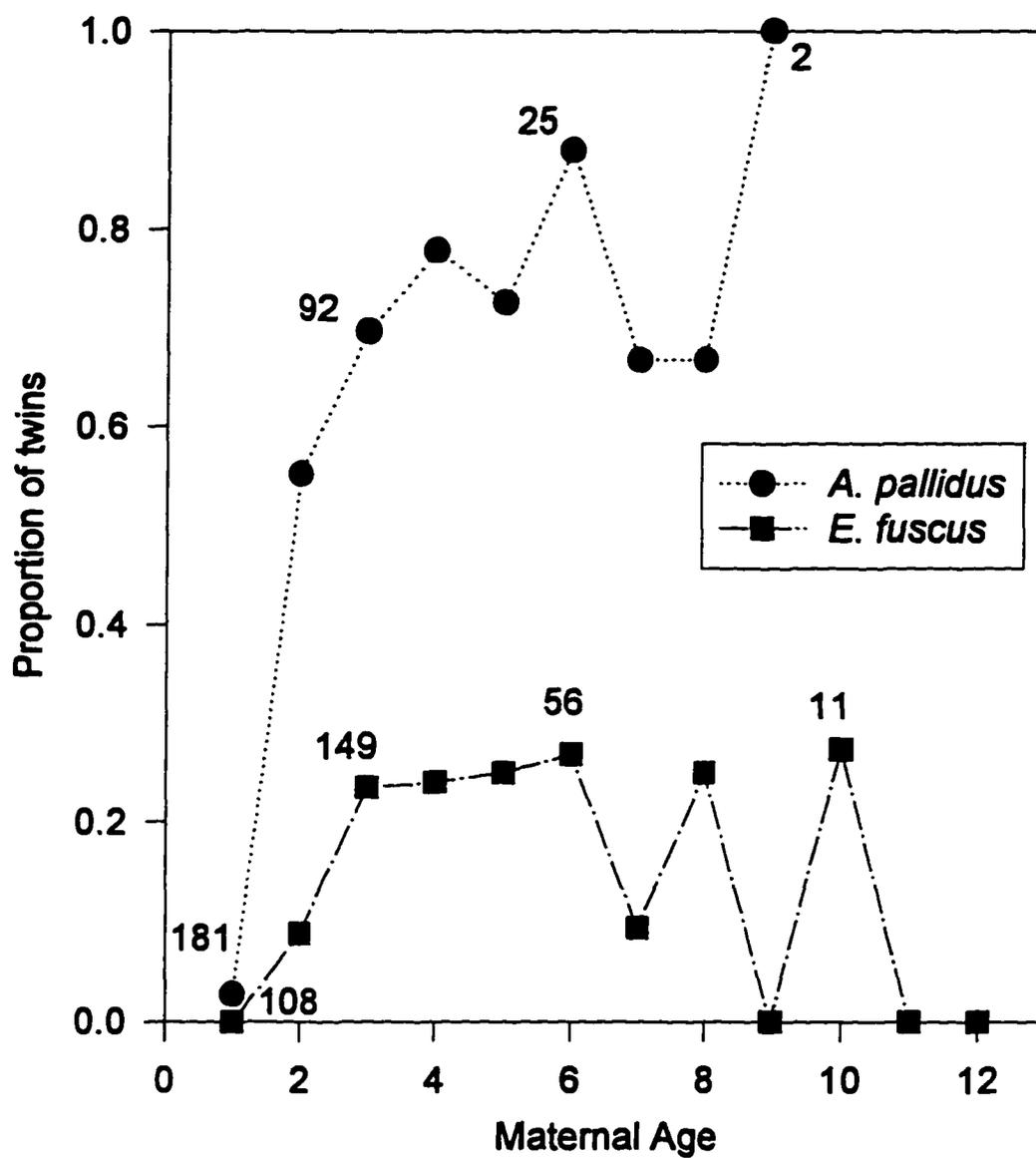


Figure 6.42-1. Proportions of twin litter production with maternal age for *A. pallidus* and *E. fuscus*. Sample sizes are indicated for some of the points.

because the sample size at this age was very small ( $n = 2$ ), and because the proportion of twins for ages seven and eight was only 67%. For *E. fuscus*, no twin litters were found for mothers aged nine, eleven, and twelve years old, but rather than this being an indication of reproductive senescence, it may be an artifact of the method of data collection (it is easier to find one young on a mother than two young-- this was especially true of *E. fuscus*; they did not have their young attached as often or as long as was the case for *A. pallidus* mothers). In fact, the highest proportion of twins was produced by ten-year old females.

Comparison of temperate versus tropical species of bats shows that most tropical species have only one young per litter; thus, larger litters are considered to be the response to lower juvenile survival during the short growing season prior to unfavorable conditions that occur in winter in temperate habitats (Barlow and Tamsitt, 1968). For temperate species that can produce twins, the immediate fitness benefit to a female that produces twins is twice as high as for a female producing only one young. Thus, if it is part of her genome to be able to do so, an adult female should produce twins (unless the increased cost of a larger litter impedes the female's survival or her chance for future reproduction).

Not all females, however, who can, do produce twins. There was definite age-dependent variation in the size of litters of both species in the current study, and an obvious question concerns the reason why. What conditions select for smaller litter

size? The most commonly proposed hypothesis supported by empirical studies of several groups of vertebrates, is that reproductive effort should decrease with a decrease in adult mortality. This hypothesis is based on the logical assumption that when the probability of adult survival is high, there should be a corresponding increase in expectation of future offspring such that it is not worth risking current survival (and therefore future reproduction) by making a big investment in current offspring, i.e., raising a big litter (Ricklefs, 1979). If this hypothesis were true, then compared to eastern populations, western *E. fuscus* should have lower annual mortality rates (or higher survival rates) in Arizona since these populations produced lower percentages of twin young than do eastern populations. In the current study, adult females in the West had higher survival rates than those reported for eastern populations (Tables 6.12-3 and 6.12-4, and Table 4-1). Perhaps higher survivorship in Arizona was due to a milder climate.

Geographical variation in litter size of *Eptesicus* has been noted not only in North America, but also for the Australian species, *E. pumilus* (McKean and Hamilton-Smith, 1967). In the U.S., some of the reported variation in litter size for *E. fuscus* includes two young per litter in central Kansas (Kunz, 1974), two young in Iowa (Kunz, 1971), two young in Massachusetts (Burnett and Kunz, 1982), two young in northwestern Texas (Jones and Manning, 1990), but one young per litter in northeastern Kansas (Phillips, 1966), one young in southern California (Cockrum,

1955), and one young in western Canada, in Alberta (Schowalter and Gunson, 1979). There are notations also in a few of these references about the unusual occurrence of one young in eastern populations of *E. fuscus* (Tuttle and Stevenson, 1982), and the rarity of two young per litter in western populations (Cockrum, 1955). In fact, Schowalter and Gunson (1979) quantified this difference when they reported that a sample of 115 pregnant females from Alberta had 13% twin young; without realizing it, they were describing not only the litter size of the population, but also some aspect of its age structure.

If eastern and western populations for *E. fuscus* have similar life span (as suggested by the known records of longevity--Sec. 6.2), then since *E. fuscus* produces two young per litter in the East and usually produces only one young in the West (Figure 6.42-1), the net productivity per female of the eastern population would be higher than that for the western population. An alternative hypothesis, that is equally reasonable, is that productivity of females in the East may decrease with age while in the West productivity increases with age, and thus productivity per female remains comparable in both populations. While there was an increase in productivity with age in these Arizona colonies (Figure 6.42-1), the evidence to test this alternative hypothesis has not yet been available for eastern populations.

Comparison of maternal productivity between the two species that share maternity roosts in this study, suggests that since this western population of *E. fuscus*

has been shown to live longer than *A. pallidus*, the average net production per female would be similar for the two species only if *A. pallidus* produces more young per litter. An analogous comparison, with similar conclusions, has been made between *E. fuscus* in Massachusetts, where this species produces two young per litter, and *Myotis lucifugus*, a species that produces one young per litter but lives longer than *E. fuscus* (Burnett and Kunz, 1982).

#### 6.43 Size of neonates

Does maternal age affect the size of young? For both *A. pallidus* and *E. fuscus*, the number of young in the litter was dependent upon the age of the mother (Figure 6.42-1). But it was necessary to determine whether the size of individual young was affected by the number of young in the litter to resolve whether mothers can influence size, and therefore, survivorship of young. Since larger young have higher survival to yearling age (Sec. 6.31), it seems reasonable to predict that this should result in selection for large young at birth. In fact, in comparison to other mammals, newborn young of bats are huge--15-30% of the mass of their mothers (Tuttle and Stevenson, 1982). Few investigations have compared the relative size of single young versus twins within individual species (Tuttle and Stevenson, 1982).

Neonates of both species (either with umbilical cords still attached to their mothers or to fresh placentae, or with dried umbilical cords still attached) that were considered to have been born within the past 24 hours (Kunz, 1974; R. Davis,

1969b) were weighed and their forearms measured, and were compared to determine differences by sex or by litter size (Tables 6.43-1 and 6.43-2). (The measurements of twin juveniles are more reliable than measurements of singleton young, because once twins are recognized by their attachment to their mother, the litter size is known definitely to be two. However, when a single juvenile is found attached to a particular mother, there is a possibility that its twin sibling was not attached at the time and the single juvenile may actually be a member of a twin litter.) Because there was a significant difference in body mass between males and females of singleton litters of *A. pallidus*, mass of singleton young were analyzed separately by sex. All other measurements were combined for sexes. The relative size of young was determined by comparing neonate size with average size of postpartum adult females that were measured within a few days after giving birth.

Female adults and young (both singleton and twin individuals) of *A. pallidus* (Table 6.43-1) were larger in absolute units of both linear measurements and body mass than *E. fuscus* (Table 6.43-2). In relative terms, i.e., comparing neonate measurements to those of postpartum adult females (using the methods of Burnett and Kunz, 1982, for eastern *E. fuscus* and *M. lucifugus*), *E. fuscus* singleton and twin young were larger than their counterparts in *A. pallidus*. This is a general trend for bats; smaller species produce relatively larger young (Tuttle and Stevenson, 1982).

Table 6.43-1. Measurements of neonatal and adult *A. pallidus*. Measurements are: FA (mm) and mass (g). Asterisks indicate tests that are significant at  $P < 0.05$ .

Neonates				
	Single Male vs Female: FA n.s.; Mass* $t = 2.48, d.f. = 13, P = 0.027$		Twin Male vs Female: FA n.s.; Mass n.s.	
	Male	Female	Male	Female
Forearm	18.9 (n = 10)	19.1 (n = 10)	17.7 (n = 20)	17.7 (n = 16)
Mass	3.71 (n = 8)	4.15 (n = 7)	3.22 (n = 14)	3.29 (n = 9)
Adults and Neonates				
	Adult (Postpartum Female)	Juvenile Single vs Twin: FA * ( $t = 3.53, d.f. = 54, P = 0.001$ ) Mass * ( $t = 5.96, d.f. = 36, P < 0.0001$ )		
		Single	Twin	
Forearm	53.8 (n = 25)	19.0 (n = 20)	17.7 (n = 36)	
Mass	19.21 (n = 25)	Male: 3.71 (n = 8) Female: 4.15 (n = 7)	3.25 (n = 23)	
Relative Size Of Young	% Adult FA	35%	33%	
	% Adult Mass	Male: 19%, Female: 22%	17%	

Table 6.43-2. Measurements of neonatal and adult *E. fuscus*. Measurements are: FA (mm) and mass (g). Asterisks indicate tests that are significant at  $P < 0.05$ .

Neonates				
	Single: FA n.s.; Mass n.s.		Twin: FA n.s.; Mass n.s.	
	Male	Female	Male	Female
Forearm	18.6 (n = 23)	18.6 (n = 7)	17.4 (n = 8)	16.5 (n = 11)
Mass	3.90 (n = 8)	4.50 (n = 2)	3.19 (n = 5)	3.09 (n = 8)
Adults and Neonates				
	Adult (Postpartum Female)	Juvenile Single vs Twin: FA * ( $t = 2.45$ , $d.f. = 47$ , $P = 0.018$ ) Mass * ( $t = 4.96$ , $d.f. = 21$ , $P < 0.0001$ )		
		Single	Twin	
Forearm	47.3 (n = 25)	18.6 (n = 30)	16.9 (n = 19)	
Mass	16.71 (n = 25)	4.02 (n = 10)	3.13 (n = 13)	
Relative Size Of Young	% Adult FA	0.39	0.36	
	% Adult Mass	0.24	0.19	

In the current study, singleton young of *A. pallidus* were significantly larger than twin individuals on both absolute and relative scales. For body mass, the sum of twins represented 34% of the postpartum female's mass as compared to 19-22% (male-female differences) for a singleton young. For *E. fuscus*, twins represented 37% of the postpartum female's mass as compared to 24% for a singleton young (Tables 6.43-1 and 6.43-2).

First-year survival was higher for singleton young of older mothers than for an individual member of a twin litter of an older mother in both species but not statistically so. (Survival rate singleton/single young of twins: *Ap*, 0.47/ 0.38; *Ef*, 0.57/ 0.46.)

It was not surprising that some females that had the physiological and genetic capability to produce twins, instead produced only one young and thus reduced their reproductive investment during some breeding attempts. It is energetically more expensive to raise two young, especially during lactation (Beasley and Leon, 1986). In addition, a single young meant a bigger young (Tables 6.43-1 and 6.43-2), and there was a survivorship advantage for bigger young (Sec. 6.31). It is possible that single young are more precocial; i.e., they can potentially reach adult size in less time than the relatively more altricial young of twin litters.

The forearm and body mass measurements of *A. pallidus* individual juveniles in this study (Table 6.43-1) were slightly larger than those reported by R. Davis

(1969b) (means for FA and mass of singletons were 19.0 mm and 3.71 g [male] or 4.15 g [female]; for individual twins these values were 17.7 mm and 3.25 g).

Measurements of twins in this study more nearly matched the juvenile measurements reported by R. Davis (1969b).

In the current study, the forearm and body mass measurements (Table 6.43-2) of individual twin *E. fuscus* (means for FA and mass were 16.9 mm and 3.13 g) were nearly identical to individual twin young of *E. fuscus* from Massachusetts (means for FA and mass were 16.8 mm and 3.3 g) and Kansas (means for FA and mass were 16.1 mm and 3.14 g). The adult females, however, were slightly larger in Arizona (47.3 mm and 16.71 g) than in Massachusetts (mean FA and mass in MA were 45.8 mm and 16.1 g; Burnett and Kunz, 1982) but smaller than postpartum females in Kansas (mean mass in KS was 19.4 g; Kunz, 1974).

The size of juveniles of both species affected their survivorship (larger juveniles had higher survivorship; Sec. 6.31), and there was no significant difference in juvenile survivorship with age of mothers (Table 6.41-1). However, maternal age affected the size of the litter (Figure 6.42-1), and the size of young was related to litter size (Tables 6.43-1 and 6.43-2). Therefore, there was an indirect effect on survivorship of young resulting from the age of the mother.

*Sex ratio.*— Another way in which mothers could affect offspring survivorship is through sex ratio adjustment (Table 6.43-3). Significant differences from the

Table 6.43-3. Offspring sex ratios for both species compared with maternal age and litter size. Maternal age in years is the known-age of cohorts originally banded as juveniles. Asterisks indicate chi-square values that are significant (at  $P < 0.05$  and  $d.f. = 2$ ) for rejecting the null hypothesis that offspring sex ratios are independent of maternal age and litter size.

<i>Antrozous pallidus</i>		Group	<i>Eptesicus fuscus</i>	
#m / #f	$\chi^2$ test for 50/50 sr		$\chi^2$ test for 50/50 sr	#m / #f
111 / 76	$\chi^2 = 5.44^*$ $P = 0.019$	Maternal age 1	$\chi^2 = 4.08^*$ $P > 0.025$	65 / 43
97 / 109	n.s.	2	n.s.	105 / 105
79 / 77	n.s.	3	n.s.	98 / 86
65 / 63	n.s.	4	n.s.	58 / 61
38 / 31	n.s.	5	n.s.	46 / 43
26 / 21	n.s.	6	n.s.	42 / 27
7 / 8	n.s.	7	n.s.	17 / 18
4 / 1	n.s.	8	n.s.	20 / 15
1 / 3	n.s.	9	n.s.	5 / 2
---	---	10	n.s.	8 / 6
---	---	11	n.s.	2 / 0
---	---	12	n.s.	4 / 1
196 / 163	n.s.	singleton	n.s.	526 / 467
407 / 393	n.s.	twins	n.s.	231 / 199
603 / 556	n.s.	total offspring	$\chi^2 = 5.69$ $P < 0.025$	757 / 666
111 / 76	$\chi^2 = 4.37$ $P = 0.037$	Yearling vs Older Mothers	n.s.	65 / 43
317 / 313				405 / 364

expected 50/50 sex ratio were found only for the yearling maternal age class of both species. For *A. pallidus* this male-biased sex ratio by yearling mothers was also significantly different than the sex ratio of offspring from all older ages classes combined, because the other age classes did not have significantly biased sex ratios. For *E. fuscus*, the significantly different sex ratio of yearling mothers was not different than offspring sex ratios for all other age classes combined, because most age classes individually showed a trend toward male-biased sex ratios (that were not statistically significant); and the overall offspring sex ratio was significantly male-biased for *E. fuscus* (Table 6.43-3).

Because this study was limited to maternity roosts (with low male return rates), there was no way to directly compare first-year survivorship between males and females. However, smaller female juveniles had lower survivorship than larger females (Sec. 6.31), and in the case of *A. pallidus*, since singleton males weighed significantly less than females, it is reasonable to assume that male juveniles have a lower first-year survivorship than females. A male-biased sex ratio would help compensate for such differences in survivorship.

#### 6.44 Age of first reproduction and longevity of females

Reproductive investment made by females was large for the production of one young and huge for the production of twins (38% and 34% of the mother's postpartum body mass of *E. fuscus* and *A. pallidus*, respectively; Tables 6.43-1 and

6.43-2). Such a nutritional and aerodynamic burden would have the potential to increase adult mortality. I predicted that *E. fuscus* females in Arizona that delayed reproduction until age two would live longer than those bearing young at age one.

The mean age before death for these two groups of adult female *E. fuscus* in the current study was not significantly different (barren at age one:  $n = 137$ , range of life span = 1-12; reproductive at age one:  $n = 112$ , range of life span = 1-13; Mann Whitney Rank Sum Test,  $T = 13057.0$ ,  $P = 0.096$ ).

Equal longevity for breeders and non-breeders was not the case for a species in another family of bats, the Rhinolophidae. In Great Britain, *Rhinolophus ferrumequinum* that bred at age two (the species does not breed at age one) had significantly lower mean age at death than females who delayed their first pregnancy until age three (Ransome, 1995). However, *R. ferrumequinum* can live and breed for 29 years, and this species produces only one young per litter (Ransome, 1995). While *Rhinolophus*, with no option for twins, must give up reproduction totally in order to decrease reproductive effort, *E. fuscus* has the additional alternative of reducing the litter size from two to one.

#### 6.45 Percent barrenness as a function of age

Selection favors early reproduction in life because there is always a finite chance of death (Pianka, 1978; Charlesworth, 1994). The initiation of reproduction is often delayed, however, suggesting that fitness benefits accrue when reproduction is

delayed. For mammals, metabolic costs are high during pregnancy and lactation, and especially for bats, because they produce such large young (Sec. 6.43). For these long-lived mammals, the high potential for future reproduction should increase the accrued benefit of postponing current reproduction if future reproductive effort is jeopardized by the current effort. For bats in the temperate zone, an important jeopardy takes the form of low fat deposition before winter hibernation.

Species such as *A. pallidus* and *E. fuscus*, that can produce twins, can decrease reproductive effort when it is beneficial by decreasing the size of the litter from two to one to none. The fact that some percentage of yearling *E. fuscus* females were barren was detected by few earlier researchers (Barbour and Davis, 1969; Schowalter and Gunson, 1979), but this observation allowed the prediction that the percentage of non-reproductive bats in each age class should decrease with increasing age since the residual reproductive value decreases with age (Burnett and Kunz, 1982).

The extent to which *E. fuscus* and *A. pallidus* deferred reproduction differed significantly between the species; more than 50% of yearling *E. fuscus*, but only 11% of yearling *A. pallidus*, were barren during yearling age (Table 6.45-1).

The combined strategies of twin production (that should be more likely to occur in populations that face high juvenile mortality, or high adult mortality outside the reproductive season) and totally deferred reproduction (that should occur in

Table 6.45-1. Percent barrenness as a function of female age in *A. pallidus* and *E. fuscus*.

<i>Antrozous pallidus</i>		Age (years)	<i>Eptesicus fuscus</i>	
% Barren	n		n	% Barren
11.5	226	1	421	54.4
4.6	151	2	387	4.7
1.0	103	3	281	3.9
1.3	76	4	204	3.4
0	45	5	145	2.8
0	67	6	101	5.0
0	11	7	76	1.3
0	3	8	53	3.8
0	2	9	26	0
---	---	10	22	0
---	---	11	12	9.1
---	---	12	9	0

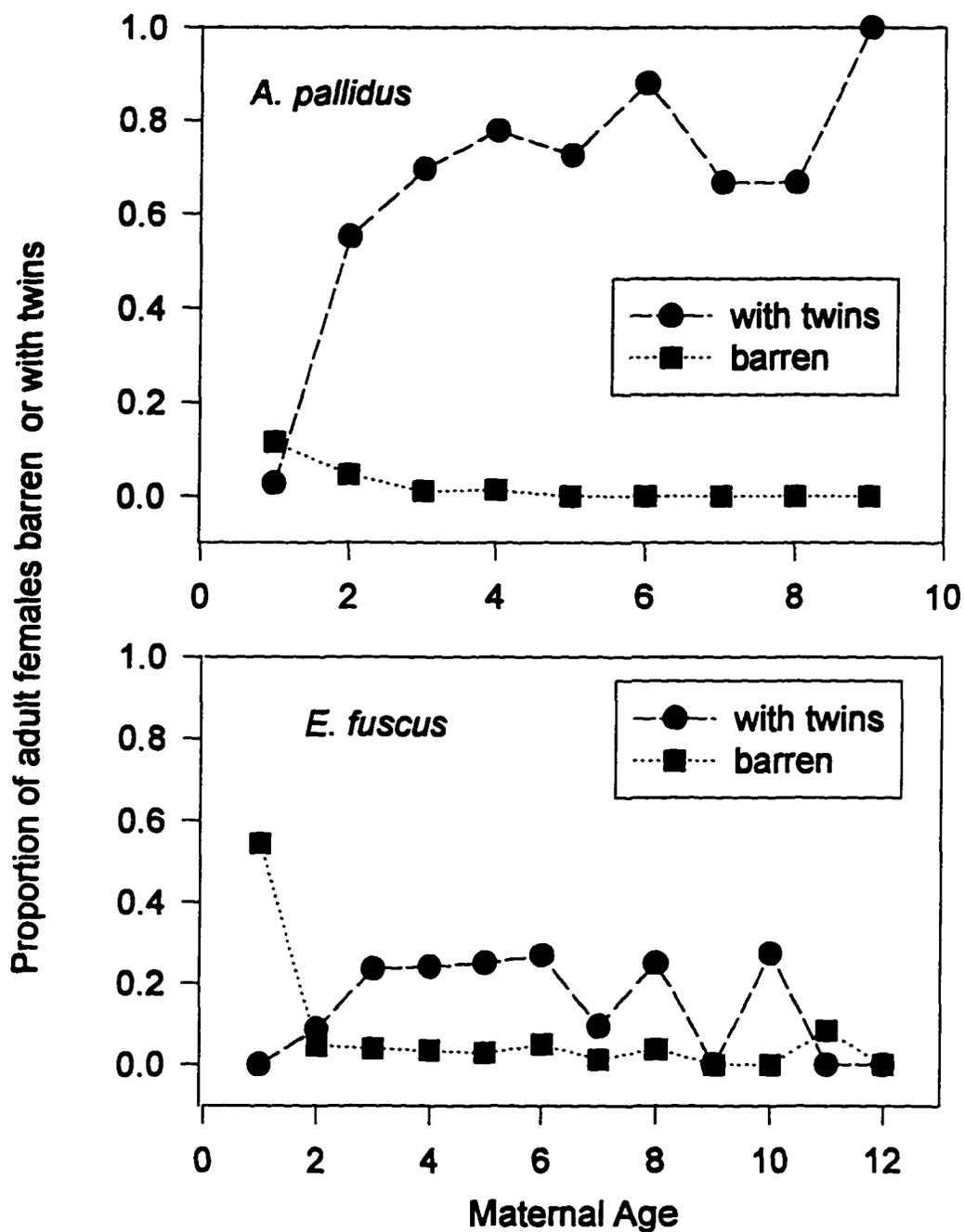


Figure 6.45-1. Comparison of reproductive strategies of adult female *A. pallidus* and *E. fuscus* in southeastern Arizona.

response to low annual adult mortality) were both observed for *A. pallidus* and *E. fuscus* in southeastern Arizona (Figure 6.45-1), but to different degrees, and with very different results.

As compared to *E. fuscus*, colonies of *A. pallidus* in this study had shorter life span, earlier age of first reproduction (i.e., almost none employed deferred reproduction (Figure 6.45-1), and larger litter size. These are life history traits that predict higher juvenile mortality, and *A. pallidus* followed the prediction (Figure 6.45-2). On the other hand, the deferment of reproduction by 54% of yearling female *E. fuscus*, and the low rate of twin production by most reproducing *E. fuscus*, are life history characters that suggest low juvenile mortality rates, and in comparison to *A. pallidus*, this also appeared to be true (Figure 6.45-1). The potential loss of fitness as a result of deferred reproduction and small litter size that were observed in *E. fuscus* was probably compensated by long life span in combination with higher juvenile survivorship (Figure 6.45-2).

Future studies of age-specific cohort analyses will show whether populations that occur elsewhere, that usually have two young per litter, have lower juvenile survivorship and/or higher adult mortality than *E. fuscus* in southeastern Arizona. A project involving *E. fuscus* survivorship has been underway for about six years in Alberta and should provide interesting intra-specific comparison with the study presented here (Barclay, 1994). The colonies in that Alberta study also use manmade

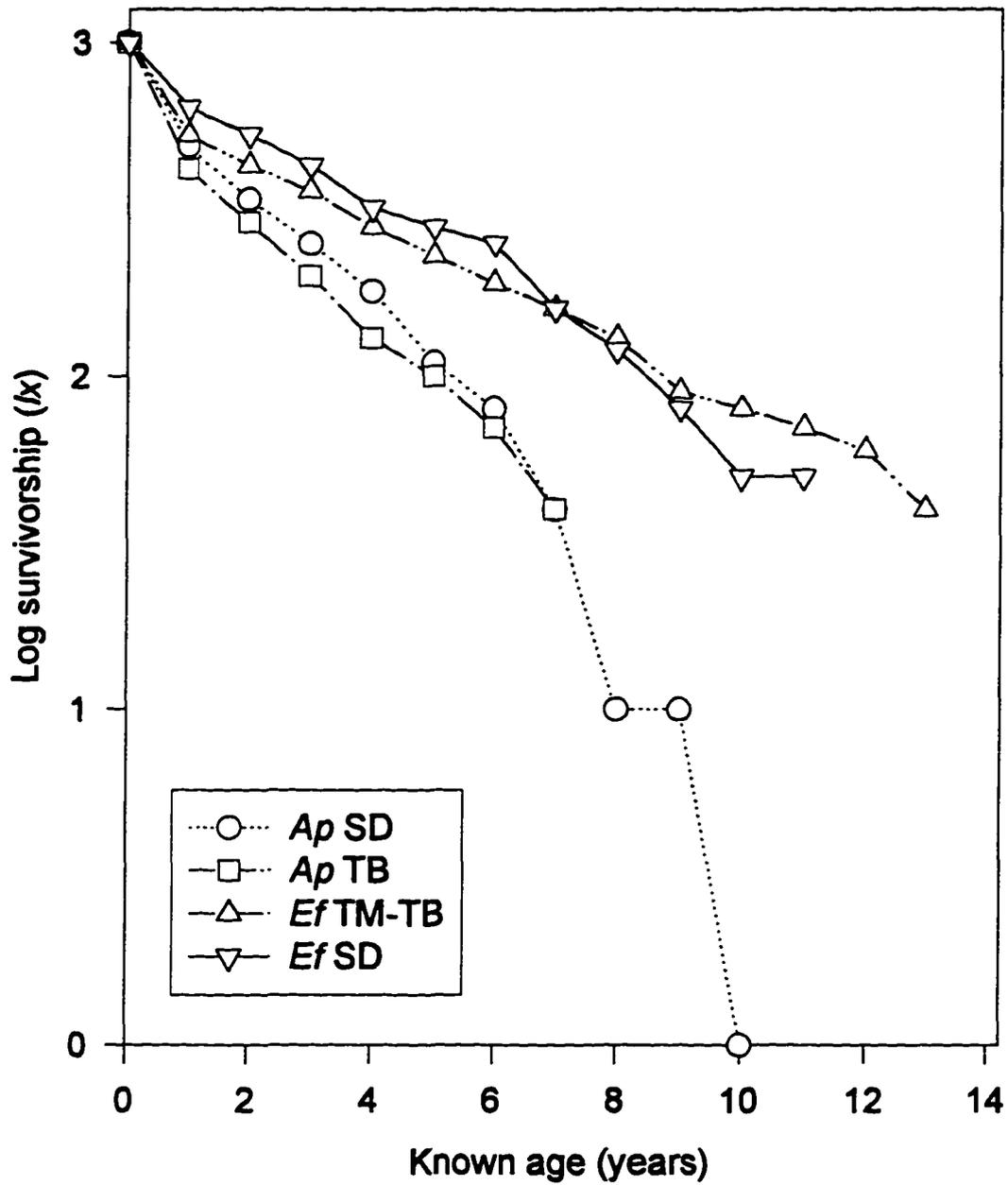


Figure 6.45-2. Comparisons of mean survivorship from combined (known-age) cohorts of female *A. pallidus* and *E. fuscus*.

structures, but because they are in buildings, where the roosts may be better protected from the kind of human destruction described for the Tombstone roosts in southeastern Arizona.

## 7. SUMMARY

In southeastern Arizona, maternity colonies of *A. pallidus* and *E. fuscus* shared manmade structures and associated environmental conditions from May to October, before moving to unknown hibernacula. Surviving female colony members returned to these roosts each Spring. Colony sizes remained relatively consistent under the influences of mortality and adult female productivity.

During 15 consecutive years of study, survivorship within and between populations of *A. pallidus* and *E. fuscus* varied considerably at the Tombstone roosts. Mean first-year survivorship was higher for known-age cohorts of *E. fuscus* than for *A. pallidus*. Second and third-year survivorship was substantially higher than first-year survivorship for both species. *Eptesicus fuscus* had higher survivorship than *A. pallidus* for the second age class also.

Both juvenile and adult female *E. fuscus* had lower mortality rates than did *A. pallidus*. At the same time, the reproductive effort of most adult *E. fuscus* females was decreased by litter size reduction and deferred age of first reproduction. Most female *A. pallidus* (88%) began having young at yearling age. At age two, 55% of *A. pallidus* females produced twin young, and at older ages as many as 100% produced twins. In contrast, 54% of *E. fuscus* females deferred their first reproduction until age two years. Only 9% of two-year old *E. fuscus* had twin young, and at older ages no more than 27% of females produced twins. The lower annual productivity by

*E. fuscus* females appeared to be balanced by longer life. While only 10% of the population of *A. pallidus* lived to reach five years of age, more than 10% of the population of *E. fuscus* attained eight years of age.

Two potential consequences of these reproductive strategies of bats are higher mortality to females that reproduce during yearling age, and higher mortality to young in twin litters because of smaller size. In this study, adult survivorship, measured as the mean age at which females were last observed, did not differ between female *E. fuscus* that produced young their first year and those that deferred reproduction until age two.

Individual young from twin litters of both *E. fuscus* and *A. pallidus* were significantly smaller than singleton young, and larger juveniles (measured on the same date) had higher first-year survivorship. Survivorship of singleton young was about 10% higher than that for a single individual from a twin litter for both species (but these differences were not statistically significant).

Yearling females of both species produce significantly male-biased offspring sex ratios, but all older age classes of both species produce equal numbers of offspring sexes. The overall sex ratios of all offspring in the study (*A. pallidus*,  $n = 1159$ ; *E. fuscus*,  $n = 1423$ ) were male-biased, but only for *E. fuscus* were these statistically significant.

By showing that the western subspecies, *E. f. pallidus*, in this study produced smaller litters, deferred its first age of reproduction, and had higher juvenile and adult survivorship than the eastern subspecies *E. f. fuscus*, I have demonstrated geographical differences in life history within a species. By comparison, eastern populations produce larger litters and are not reported to defer first age of reproduction, and they have lower reported survivorship.

Maximum life span records for *A. pallidus* reported in this study included two females banded as juveniles that lived to nine years, and two females banded as adults, of which one lived to be at least 10 years old and the other was at least 11 when last observed. An adult male that was recaptured from a previous study was ten years old. Only one cohort of *E. fuscus* was followed for sufficient time to allow all its members to complete their life spans. Within the time that was available, the oldest known-age individuals in this study were four females that reached 13 years of age. Of two females banded as adults, one lived to be at least 14 years old, and the other was at least 15 when last observed.

Known causes of mortality in bats that were observed in this study included disease, predation, inclement weather, and human disturbance. A small proportion of these bats incubate rabies and must eventually succumb to it. Predation by spotted owls on these two species has been documented in southern Arizona, and one banded male *E. fuscus* juvenile from the TB roost was found in a spotted owl pellet in the

Huachuca Mountains in winter. Summer rainstorms were found to have a statistically significant negative effect on juvenile survivorship of *A. pallidus*, as did human disturbance at these roosts. By far, the greatest measured mortality at these roosts was caused by human vandals. Three episodes of human destruction were discovered that caused potential reductions of 17-23% of adult female *E. fuscus* at TB, 23-34% at SD, and 100% of the *A. pallidus* colony at TB.

Even though they occur at different points on the continuum of iteroparous breeding patterns of mammals, these two species have evolved a life history that allows reproductive replacement with lower fecundity and higher survivorship than would be predicted from body size.

The life history traits of the two species and/or the factors that influenced them are summarized in Table 7-1.

Table 7-1. Summary comparison of life history traits between *A. pallidus* and *E. fuscus*. These traits and/or factors influencing their life history were determined from data obtained in this study. For a comparison of other traits of the species, see Hermanson and O'Shea (1983) and Kurta and Baker (1990).

Trait	<i>A. pallidus</i>	<i>E. fuscus pallidus</i>
1. Survivorship	age-specific	age-specific
2. Mean (and range) of first-year (juvenile) survivorship for individual cohorts	0.46 (0.18-0.74)	0.56 (0.30-0.77)
3. First-year survivorship	significantly lower	significantly higher
4. Mean (and range) of second-year (adult) survivorship for individual cohorts	0.66 (0.08-0.86)	0.80 (0.43-1.00)
5. Second-year survivorship	significantly lower	significantly higher
6. Mean first-year survivorship compared to adult survivorship	significantly lower	significantly lower
7. Mean (and range) of third-year survivorship; no significant difference between species	0.78 (0.44-1.00)	0.80 (0.67-0.93)
8. Maximum life span	female $\geq$ 11 years male = 10 years	female $\geq$ 15 years
9. Age at which 90% of population has died	5 years	8 years
10. Influence of a roost on first-year survivorship	significantly higher at SD Roost	significantly higher at SD roost
11. Relationship of summer rainfall on first-year survivorship	influence is weak and inversely proportional	not statistically significant
12. Timing of parturition	earlier (2nd through last wk of June)	later (last wk of June through 2nd wk July)
13. Evidence of predation by spotted owls	yes	yes

Table 7-1 *continued*

14. Occurrence of band damage	4%	15%
15. Number of young produced per year by one-year old mothers that do not defer reproduction	one	one
16. Percent of females that defer age of first reproduction to 2-years of age	12%	54%
17. Percent of two-year old mothers having twins	55%	9%
18. Highest percent of mothers of any age having twins	100% (age 9 years)	27% (ages 6 and 10 years)
19. Mean size of postpartum females	FA 53.8 mm Mass 19.21 g	FA 47.3 mm Mass 16.71 g
20. Comparative size of neonates	larger in absolute size, smaller in relative size	smaller in absolute size, larger in relative size
21. Individual neonate size relative to mass of postpartum female	Single 19 and 22% (male and female) Twin 17%	Single 24% Twin 19%
22. Offspring sex ratios of yearling mothers	significantly male-biased	significantly male-biased
23. Offspring sex ratios of mothers older than 1 year	50/50	50/50
24. Total offspring sex ratios	male-biased	significantly male-biased

**8. APPENDIX A: ANIMAL SUBJECTS APPROVAL**

Institutional Animal Care  
and Use Committee

THE UNIVERSITY OF  
**ARIZONA.**  
TUCSON ARIZONA

Tucson, Arizona 85721

Verification of Review  
By The Institutional Animal Care and Use Committee (IACUC)

***Final Approval Granted***

PHS Assurance No. A-3248-01 – USDA No. 86-3

TITLE: PROTOCOL CONTROL # 97-043

**“Field Studies of Bats in Southeastern Arizona”**

PRINCIPAL INVESTIGATOR/DEPARTMENT:

**Rhonda Marie Sidner - Ecology & Evolutionary Biology**

SUBMISSION DATE: March 20, 1997

APPROVAL DATE: April 15, 1997

GRANTING AGENCY:

**Non-Sponsored - Dissertation Project**

The University of Arizona Institutional Animal Care and Use Committee reviews all sections of proposals relating to animal care and use. The above named proposal has been granted Final Approval according to the review policies of the IACUC.

NOTES:

\*\*\* Full approval of this control number is valid through\*: April 14, 2000

\* When projects or grant periods extend past the above noted expiration date, the Principal Investigator will submit a new protocol proposal for full review. Following IACUC review, a new Protocol Control Number and Expiration Date will be assigned.

\*\*\* Continued approval for this project was confirmed: April 15, 1997

\*\*\* Revisions (if any), are listed below:



Michael A. Cusanovich, Ph.D.  
Vice President for Research

DATE: April 15, 1997

## 9. APPENDIX B: LIFE TABLES FROM KNOWN-AGE COHORTS.

This appendix contains life tables from individual known-age cohorts that are provided in addition to those that appear in Sec. 6.11.

Column headings in the tables are explained below (from Caughley, 1977):

Year  $x$ —the year that bats of any cohort are counted.

Age—the actual age (in years) of members of the cohort that were first banded at age 0, as juveniles. Age is  $x$  at age 0, then  $x+1$  at age 1, and so on...

Freq.  $f_x$ —frequency; the number of surviving bats in the cohort at age  $x$ , and  $x+1$ , and so on...

Surviv.  $l_x$ —survival; the probability at birth of surviving to age  $x$ , and  $x+1$ , and so on... (the number of bats surviving compared to those in the age 0 class).

Mortal.  $d_x$ —mortality; the probability of dying in each age interval  $x$ ,  $x+1$ , and so on... (the difference between  $l_x$  at age  $x$  and age  $x+1$ , age  $x+1$  and  $x+2$ , and so on...).

Mort.Rt.  $q_x$ —mortality rate;  $d_x$  at age  $x/l_x$  at age  $x$ ,  $d_x$  at age  $x+1/l_x$  at age  $x+1$ , and so on...

Surv.Rt.  $p_x$ —survival rate;  $1-q_x$  at age  $x$ ,  $1-q_x$  at age  $x+1$ , and so on...

Table B.1 Life table from the known-age cohort of *A. pallidus* at SD in 1980.

Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1980	0	50	1.000	0.260	0.260	0.740
1981	1	37	0.740	0.200	0.270	0.730
1982	2	27	0.540	0.300	0.556	0.444
1983	3	12	0.240	0.040	0.167	0.833
1984	4	10	0.200	0.140	0.700	0.300
1985	5	3	0.060	0.020	0.333	0.667
1986	6	2	0.040	0.020	0.500	0.500
1987	7	1	0.020	0.020	1.000	0.000
1988	8	0	0			

Table B.2 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1981.

SD						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1981	0	28	1.000	0.571	0.571	0.429
1982	1	12	0.429	0.071	0.167	0.833
1983	2	10	0.357	0.000	0.000	1.000
1984	3	10	0.357	0.214	0.600	0.400
1985	4	4	0.143	0.036	0.250	0.750
1986	5	3	0.107	0.071	0.667	0.333
1987	6	1	0.036	0.036	1.000	0.000
1988	7	0	0			

TB						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1981	0	23	1.000	0.565	0.565	0.435
1982	1	10	0.435	0.130	0.300	0.700
1983	2	7	0.304	0.087	0.286	0.714
1984	3	5	0.217	0.087	0.400	0.600
1985	4	3	0.130	0.043	0.333	0.667
1986	5	2	0.087	0.043	0.500	0.500
1987	6	1	0.043	0.000	0.000	1.000
1988	7	1	0.043	0.043	1.000	0.000
1989	8	0	0			

Table B.3 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1982.

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1982	0	32	1.000	0.313	0.313	0.688
1983	1	22	0.688	0.094	0.136	0.864
1984	2	19	0.594	0.156	0.263	0.737
1985	3	14	0.438	0.094	0.214	0.786
1986	4	11	0.344	0.125	0.364	0.636
1987	5	7	0.219	0.031	0.143	0.857
1988	6	6	0.188	0.094	0.500	0.500
1989	7	3	0.094	0.063	0.667	0.333
1990	8	1	0.031	0.000	0.000	1.000
1991	9	1	0.031	0.031	1.000	0.000
1992	10	0	0			

TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1982	0	35	1.000	0.400	0.400	0.600
1983	1	21	0.600	0.171	0.286	0.714
1984	2	15	0.429	0.143	0.333	0.667
1985	3	10	0.286	0.029	0.100	0.900
1986	4	9	0.257	0.086	0.333	0.667
1987	5	6	0.171	0.086	0.500	0.500
1988	6	3	0.086	0.057	0.667	0.333
1989	7	1	0.029	0.029	1.000	0.000
1990	8	0	0			

Table B.4 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1983.

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**SD**

Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1983	0	28	1.000	0.536	0.536	0.464
1984	1	13	0.464	0.429	0.923	0.077
1985	2	1	0.036	0.000	0.000	1.000
1986	3	1	0.036	0.000	0.000	1.000
1987	4	1	0.036	0.000	0.000	1.000
1988	5	1	0.036	0.036	1.000	0.000
1989	6	0	0			

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**TB**

Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1983	0	28	1.000	0.821	0.821	0.179
1984	1	5	0.179	0.107	0.600	0.400
1985	2	2	0.071	0.000	0.000	1.000
1986	3	2	0.071	0.036	0.500	0.500
1987	4	1	0.036	0.000	0.000	1.000
1988	5	1	0.036	0.036	1.000	0.000
1989	6	0	0			

---

Table B.5 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1984.

SD						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1984	0	44	1.000	0.818	0.818	0.182
1985	1	8	0.182	0.045	0.250	0.750
1986	2	6	0.136	0.045	0.333	0.667
1987	3	4	0.091	0.000	0.000	1.000
1988	4	4	0.091	0.068	0.750	0.250
1989	5	1	0.023	0.000	0.000	1.000
1990	6	1	0.023	0.023	1.000	0.000
1991	7	0	0			

TB						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1984	0	18	1.000	0.778	0.778	0.222
1985	1	4	0.222	0.111	0.500	0.500
1986	2	2	0.111	0.000	0.000	1.000
1987	3	2	0.111	0.056	0.500	0.500
1988	4	1	0.056	0.056	1.000	0.000
1989	5	0	0			

Table B.6 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1985.

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1985	0	23	1.000	0.435	0.435	0.565
1986	1	13	0.565	0.217	0.385	0.615
1987	2	8	0.348	0.087	0.250	0.750
1988	3	6	0.261	0.043	0.167	0.833
1989	4	5	0.217	0.043	0.200	0.800
1990	5	4	0.174	0.000	0.000	1.000
1991	6	4	0.174	0.130	0.750	0.250
1992	7	1	0.043	0.000	0.000	1.000
1993	8	1	0.043	0.000	0.000	1.000
1994	9	1	0.043	0.043	1.000	0.000
1995	10	0	0			

TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1985	0	19	1.000	0.421	0.421	0.579
1986	1	11	0.579	0.158	0.273	0.727
1987	2	8	0.421	0.158	0.375	0.625
1988	3	5	0.263	0.211	0.800	0.200
1989	4	1	0.053	0.053	1.000	0.000
1990	5	0	0			

Table B.7 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1986.

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1986	0	25	1.000	0.760	0.760	0.240
1987	1	6	0.240	0.040	0.167	0.833
1988	2	5	0.200	0.080	0.400	0.600
1989	3	3	0.120	0.080	0.667	0.333
1990	4	1	0.040	0.040	1.000	0.000
1991	5	0	0			

TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1986	0	17	1.000	0.471	0.471	0.529
1987	1	9	0.529	0.176	0.333	0.667
1988	2	6	0.353	0.294	0.833	0.167
1989	3	1	0.059	0.059	1.000	0.000
1990	4	0	0			

Table B.8 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1987.

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1987	0	30	1.000	0.500	0.500	0.500
1988	1	15	0.500	0.233	0.467	0.533
1989	2	8	0.267	0.067	0.250	0.750
1990	3	6	0.200	0.033	0.167	0.833
1991	4	5	0.167	0.067	0.400	0.600
1992	5	3	0.100	0.033	0.333	0.667
1993	6	2	0.067	0.000	0.000	1.000
1994	7	2	0.067	0.067	1.000	0.000
1995	8	0	0			

TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1987	0	25	1.000	0.640	0.640	0.360
1988	1	9	0.360	0.240	0.667	0.333
1989	2	3	0.120	0.120	1.000	0.000
1990	3	0	0.000			

Table B.9 Life tables from known-age cohorts of *A. pallidus* at SD and TB in 1988.

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1988	0	29	1.000	0.379	0.379	0.621
1989	1	18	0.621	0.172	0.278	0.722
1990	2	13	0.448	0.103	0.231	0.769
1991	3	10	0.345	0.138	0.400	0.600
1992	4	6	0.207	0.000	0.000	1.000
1993	5	6	0.207	0.034	0.167	0.833
1994	6	5	0.172	0.034	0.200	0.800
1995	7	4	0.138			

TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1988	0	17	1.000	0.941	0.941	0.059
1989	1	1	0.059	0.059	1.000	0.000
1990	2	0	0.000			

Table B.10 Life tables from known age cohorts of *A. pallidus* at SD in 1989 and 1990.

SD 1989						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $q_x$	SurvRt $p_x$
1989	0	31	1.000	0.516	0.516	0.484
1990	1	15	0.484	0.161	0.333	0.667
1991	2	10	0.323	0.000	0.000	1.000
1992	3	10	0.323	0.097	0.300	0.700
1993	4	7	0.226	0.032	0.143	0.857
1994	5	6	0.194	0.032	0.167	0.833
1995	6	5	0.161			

SD 1990						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $q_x$	SurvRt $p_x$
1990	0	35	1.000	0.600	0.600	0.400
1991	1	14	0.400	0.086	0.214	0.786
1992	2	11	0.314	0.029	0.091	0.909
1993	3	10	0.286	0.000	0.000	1.000
1994	4	10	0.286	0.171	0.600	0.400
1995	5	4	0.114			

Table B.11 Life tables from known-age cohorts of *A. pallidus* at SD in 1991 and 1992.

SD 1991						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1991	0	35	1.000	0.543	0.543	0.457
1992	1	16	0.457	0.143	0.313	0.688
1993	2	11	0.314	0.086	0.273	0.727
1994	3	8	0.229	0.086	0.375	0.625
1995	4	5	0.143			

SD 1992						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1992	0	42	1.000	0.429	0.429	0.571
1993	1	24	0.571	0.119	0.208	0.792
1994	2	19	0.452	0.167	0.368	0.632
1995	3	12	0.286			

Table B.12 Life table from the known-age cohort of *E. fuscus* at TM in 1981.

Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1981	0	47	1.000	0.702	0.702	0.298
1982	1	14	0.298	0.043	0.143	0.857
1983	2	12	0.255	0.064	0.250	0.750
1984	3	9	0.191	0.043	0.222	0.778
1985	4	7	0.149	0.021	0.143	0.857
1986	5	6	0.128	0.021	0.167	0.833
1987	6	5	0.106	0.021	0.200	0.800
1988	7	4	0.085	0.021	0.250	0.750
1989	8	3	0.064	0.021	0.333	0.667
1990	9	2	0.043	0.000	0.000	1.000
1991	10	2	0.043	0.021	0.500	0.500
1992	11	1	0.021	0.000	0.000	1.000
1993	12	1	0.021	0.021	1.000	0.000
1994	13	0	0			

Table B.13 Life table from the known-age cohort of *E. fuscus* at TM in 1982.

Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1982	0	60	1.000	0.283	0.283	0.717
1983	1	43	0.717	0.117	0.163	0.837
1984	2	36	0.600	0.050	0.083	0.917
1985	3	33	0.550	0.067	0.121	0.879
1986	4	29	0.483	0.033	0.069	0.931
1987	5	27	0.450	0.033	0.074	0.926
1988	6	25	0.417	0.067	0.160	0.840
1989	7	21	0.350	0.050	0.143	0.857
1990	8	18	0.300	0.117	0.389	0.611
1991	9	11	0.183	0.017	0.091	0.909
1992	10	10	0.167	0.000	0.000	1.000
1993	11	10	0.167	0.033	0.200	0.800
1994	12	8	0.133	0.067	0.500	0.500
1995	13	4	0.067			

Table B.14 Life table from the known-age cohort of *E. fuscus* at TM-TB in 1983.

Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1983	0	64	1.000	0.500	0.500	0.500
1984	1	32	0.500	0.109	0.219	0.781
1985	2	25	0.391	0.078	0.200	0.800
1986	3	20	0.313	0.078	0.250	0.750
1987	4	15	0.234	0.047	0.200	0.800
1988	5	12	0.188	0.031	0.167	0.833
1989	6	10	0.156	0.031	0.200	0.800
1990	7	8	0.125	0.031	0.250	0.750
1991	8	6	0.094	0.000	0.000	1.000
1992	9	6	0.094	0.016	0.167	0.833
1993	10	5	0.078	0.016	0.200	0.800
1994	11	4	0.063	0.031	0.500	0.500
1995	12	2	0.031			

Table B.15 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1984.

TM-TB						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1984	0	72	1.000	0.514	0.514	0.486
1985	1	35	0.486	0.139	0.286	0.714
1986	2	25	0.347	0.042	0.120	0.880
1987	3	22	0.306	0.097	0.318	0.682
1988	4	15	0.208	0.014	0.067	0.933
1989	5	14	0.194	0.042	0.214	0.786
1990	6	11	0.153	0.014	0.091	0.909
1991	7	10	0.139	0.042	0.300	0.700
1992	8	7	0.097	0.014	0.143	0.857
1993	9	6	0.083	0.014	0.167	0.833
1994	10	5	0.069	0.042	0.600	0.400
1995	11	2	0.028			

SD						
Year	Age $x$	Freq $fx$	Surviv $lx$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1984	0	20	1.000	0.600	0.600	0.400
1985	1	8	0.400	0.100	0.250	0.750
1986	2	6	0.300	0.100	0.333	0.667
1987	3	4	0.200	0.050	0.250	0.750
1988	4	3	0.150	0.000	0.000	1.000
1989	5	3	0.150	0.000	0.000	1.000
1990	6	3	0.150	0.100	0.667	0.333
1991	7	1	0.050	0.000	0.000	1.000
1992	8	1	0.050	0.000	0.000	1.000
1993	9	1	0.050	0.000	0.000	1.000
1994	10	1	0.050	0.000	0.000	1.000
1995	11	1	0.050			

Table B.16 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1985.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1985	0	67	1.000	0.522	0.522	0.478
1986	1	32	0.478	0.179	0.375	0.625
1987	2	20	0.299	0.060	0.200	0.800
1988	3	16	0.239	0.075	0.313	0.688
1989	4	11	0.164	0.045	0.273	0.727
1990	5	8	0.119	0.000	0.000	1.000
1991	6	8	0.119	0.015	0.125	0.875
1992	7	7	0.104	0.030	0.286	0.714
1993	8	5	0.075	0.030	0.400	0.600
1994	9	3	0.045	0.000	0.000	1.000
1995	10	3	0.045			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1985	0	17	1.000	0.588	0.588	0.412
1986	1	7	0.412	0.235	0.571	0.429
1987	2	3	0.176	0.059	0.333	0.667
1988	3	2	0.118	0.000	0.000	1.000
1989	4	2	0.118	0.059	0.500	0.500
1990	5	1	0.059	0.000	0.000	1.000
1991	6	1	0.059	0.000	0.000	1.000
1992	7	1	0.059	0.000	0.000	1.000
1993	8	1	0.059	0.000	0.000	1.000
1994	9	1	0.059	0.000	0.000	1.000
1995	10	1	0.059			

Table B.17 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1986.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1986	0	66	1.000	0.561	0.561	0.439
1987	1	29	0.439	0.061	0.138	0.862
1988	2	25	0.379	0.061	0.160	0.840
1989	3	21	0.318	0.076	0.238	0.762
1990	4	16	0.242	0.030	0.125	0.875
1991	5	14	0.212	0.000	0.000	1.000
1992	6	14	0.212	0.030	0.143	0.857
1993	7	12	0.182	0.030	0.167	0.833
1994	8	10	0.152	0.045	0.300	0.700
1995	9	7	0.106			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1986	0	13	1.000	0.462	0.462	0.538
1987	1	7	0.538	0.154	0.286	0.714
1988	2	5	0.385	0.077	0.200	0.800
1989	3	4	0.308	0.000	0.000	1.000
1990	4	4	0.308	0.000	0.000	1.000
1991	5	4	0.308	0.077	0.250	0.750
1992	6	3	0.231	0.000	0.000	1.000
1993	7	3	0.231	0.000	0.000	1.000
1994	8	3	0.231	0.077	0.333	0.667
1995	9	2	0.154			

Table B.18 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1987.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1987	0	72	1.000	0.500	0.500	0.500
1988	1	36	0.500	0.167	0.333	0.667
1989	2	24	0.333	0.083	0.250	0.750
1990	3	18	0.250	0.111	0.444	0.556
1991	4	10	0.139	0.000	0.000	1.000
1992	5	10	0.139	0.014	0.100	0.900
1993	6	9	0.125	0.000	0.000	1.000
1994	7	9	0.125	0.014	0.111	0.889
1995	8	8	0.111			

SD						
Year	Age	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1987	0	23	1.000	0.522	0.522	0.478
1988	1	11	0.478	0.000	0.000	1.000
1989	2	11	0.478	0.087	0.182	0.818
1990	3	9	0.391	0.043	0.111	0.889
1991	4	8	0.348	0.000	0.000	1.000
1992	5	8	0.348	0.043	0.125	0.875
1993	6	7	0.304	0.087	0.286	0.714
1994	7	5	0.217	0.043	0.200	0.800
1995	8	4	0.174			

Table B.19 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1988.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1988	0	69	1.000	0.565	0.565	0.435
1989	1	30	0.435	0.072	0.167	0.833
1990	2	25	0.362	0.087	0.240	0.760
1991	3	19	0.275	0.043	0.158	0.842
1992	4	16	0.232	0.000	0.000	1.000
1993	5	16	0.232	0.014	0.063	0.938
1994	6	15	0.217	0.043	0.200	0.800
1995	7	12	0.174			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1988	0	19	1.000	0.263	0.263	0.737
1989	1	14	0.737	0.211	0.286	0.714
1990	2	10	0.526	0.053	0.100	0.900
1991	3	9	0.474	0.053	0.111	0.889
1992	4	8	0.421	0.105	0.250	0.750
1993	5	6	0.316	0.053	0.167	0.833
1994	6	5	0.263	0.000	0.000	1.000
1995	7	5	0.263			

Table B.20 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1989.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1989	0	55	1.000	0.400	0.400	0.600
1990	1	33	0.600	0.091	0.152	0.848
1991	2	28	0.509	0.036	0.071	0.929
1992	3	26	0.473	0.055	0.115	0.885
1993	4	23	0.418	0.091	0.217	0.783
1994	5	18	0.327	0.127	0.389	0.611
1995	6	11	0.200			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $qx$	SurvRt $px$
1989	0	34	1.000	0.235	0.235	0.765
1990	1	26	0.765	0.059	0.077	0.923
1991	2	24	0.706	0.118	0.167	0.833
1992	3	20	0.588	0.088	0.150	0.850
1993	4	17	0.500	0.029	0.059	0.941
1994	5	16	0.471	0.118	0.250	0.750
1995	6	12	0.353			

Table B.21 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1990.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $q_x$	SurvRt $p_x$
1990	0	81	1.000	0.457	0.457	0.543
1991	1	44	0.543	0.037	0.068	0.932
1992	2	41	0.506	0.049	0.098	0.902
1993	3	37	0.457	0.037	0.081	0.919
1994	4	34	0.420	0.136	0.324	0.676
1995	5	23	0.284			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $dx$	MortRt $q_x$	SurvRt $p_x$
1990	0	25	1.000	0.280	0.280	0.720
1991	1	18	0.720	0.160	0.222	0.778
1992	2	14	0.560	0.080	0.143	0.857
1993	3	12	0.480	0.200	0.417	0.583
1994	4	7	0.280	0.080	0.286	0.714
1995	5	5	0.200			

Table B.22 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1991.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1991	0	65	1.000	0.446	0.446	0.554
1992	1	36	0.554	0.015	0.028	0.972
1993	2	35	0.538	0.077	0.143	0.857
1994	3	30	0.462	0.092	0.200	0.800
1995	4	24	0.369			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1991	0	18	1.000	0.278	0.278	0.722
1992	1	13	0.722	0.111	0.154	0.846
1993	2	11	0.611	0.167	0.273	0.727
1994	3	8	0.444	0.167	0.375	0.625
1995	4	5	0.278			

Table B.23 Life tables from known-age cohorts of *E. fuscus* at TM-TB and SD in 1992.

TM-TB						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1992	0	75	1.000	0.280	0.280	0.720
1993	1	54	0.720	0.080	0.111	0.889
1994	2	48	0.640	0.213	0.333	0.667
1995	3	32	0.427			

SD						
Year	Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1992	0	46	1.000	0.261	0.261	0.739
1993	1	34	0.739	0.065	0.088	0.912
1994	2	31	0.674	0.152	0.226	0.774
1995	3	24	0.522			

## 10. APPENDIX C: LIFE TABLES FROM UNKNOWN-AGE COHORTS.

This appendix includes life tables of individual cohorts from unknown-age adults of both *A. pallidus* and *E. fuscus* that are the source of the oldest known bats in the study, as described in Sec. 6.2 (Longevity). Column headings are as described in Appendix B, except here, Bd-Age  $x$  is the age assigned at banding when the actual age was unknown but was  $\geq 1$  when the bat was first banded as an adult.

Table C.1 Life tables from unknown-age cohorts of *A. pallidus* at SD in 1980 and TB in 1981.

SD 1980						
Year	Bd-Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1980	0 (> 1)	73	1.000	0.178	0.178	0.822
1981	1 (> 2)	60	0.822	0.260	0.317	0.683
1982	2 (> 3)	41	0.562	0.219	0.390	0.610
1983	3 (> 4)	25	0.342	0.027	0.080	0.920
1984	4 (> 5)	23	0.315	0.247	0.783	0.217
1985	5 (> 6)	5	0.068	0.027	0.400	0.600
1986	6 (> 7)	3	0.041	0.000	0.000	1.000
1987	7 (> 8)	3	0.041	0.014	0.333	0.667
1988	8 (> 9)	2	0.027	0.000	0.000	1.000
1989	9 (> 10)	2	0.027	0.014	0.500	0.500
1990	10 (> 11)	1	0.014	0.014	1.000	0.000
1991	11 (> 12)	0	0			

TB 1981						
Year	Bd-Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1981	0 (> 1)	34	1.000	0.206	0.206	0.794
1982	1 (> 2)	27	0.794	0.294	0.370	0.630
1983	2 (> 3)	17	0.500	0.029	0.059	0.941
1984	3 (> 4)	16	0.471	0.265	0.563	0.438
1985	4 (> 5)	7	0.206	0.088	0.429	0.571
1986	5 (> 6)	4	0.118	0.029	0.250	0.750
1987	6 (> 7)	3	0.088	0.059	0.667	0.333
1988	7 (> 8)	1	0.029	0.029	1.000	0.000
1989	8 (> 9)	0	0			

Table C.2 Life table from the unknown-age cohort of *E. fuscus* adults at TM in 1981.

Year	Bd-Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1981	0 (>1)	77	1.000	0.195	0.195	0.805
1982	1 (>2)	62	0.805	0.156	0.194	0.806
1983	2 (>3)	50	0.649	0.078	0.120	0.880
1984	3 (>4)	44	0.571	0.143	0.250	0.750
1985	4 (>5)	33	0.429	0.052	0.121	0.879
1986	5 (>6)	29	0.377	0.104	0.276	0.724
1987	6 (>7)	21	0.273	0.039	0.143	0.857
1988	7 (>8)	18	0.234	0.104	0.444	0.556
1989	8 (>9)	10	0.130	0.026	0.200	0.800
1990	9 (>10)	8	0.104	0.026	0.250	0.750
1991	10 (>11)	6	0.078	0.013	0.167	0.833
1992	11 (>12)	5	0.065	0.000	0.000	1.000
1993	12 (>13)	5	0.065	0.039	0.600	0.400
1994	13 (>14)	2	0.026	0.013	0.500	0.500
1995	14 (>15)	1	0.013	0.013	1.000	0.000

Table C.3 Life tables from unknown-age cohorts of *E. fuscus* adults at TM in 1982 and SD in 1984.

TM 1982						
Year	Bd-Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1982	0 (> 1)	33	1.000	0.273	0.273	0.727
1983	1 (> 2)	24	0.727	0.121	0.167	0.833
1984	2 (> 3)	20	0.606	0.121	0.200	0.800
1985	3 (> 4)	16	0.485	0.121	0.250	0.750
1986	4 (> 5)	12	0.364	0.152	0.417	0.583
1987	5 (> 6)	7	0.212	0.030	0.143	0.857
1988	6 (> 7)	6	0.182	0.091	0.500	0.500
1989	7 (> 8)	3	0.091	0.030	0.333	0.667
1990	8 (> 9)	2	0.061	0.030	0.500	0.500
1991	9 (> 10)	1	0.030	0.000	0.000	1.000
1992	10 (> 11)	1	0.030	0.000	0.000	1.000
1993	11 (> 12)	1	0.030	0.000	0.000	1.000
1994	12 (> 13)	1	0.030	0.030	1.000	0.000
1995	13 (> 14)	0	0.000			

SD 1984						
Year	Bd-Age $x$	Freq $f_x$	Surviv $l_x$	Mortal $d_x$	MortRt $q_x$	SurvRt $p_x$
1984	0 (> 1)	20	1.000	0.200	0.200	0.800
1985	1 (> 2)	16	0.800	0.250	0.313	0.688
1986	2 (> 3)	11	0.550	0.050	0.091	0.909
1987	3 (> 4)	10	0.500	0.100	0.200	0.800
1988	4 (> 5)	8	0.400	0.000	0.000	1.000
1989	5 (> 6)	8	0.400	0.050	0.125	0.875
1990	6 (> 7)	7	0.350	0.000	0.000	1.000
1991	7 (> 8)	7	0.350	0.050	0.143	0.857
1992	8 (> 9)	6	0.300	0.050	0.167	0.833
1993	9 (> 10)	5	0.250	0.100	0.400	0.600
1994	10 (> 11)	3	0.150	0.000	0.000	1.000
1995	11 (> 12)	3	0.150	0.150	1.000	0.000

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