SPECIES ASSESSMENT FOR TOWNSEND'S BIG-EARED BAT (CORYNORHINUS [=PLECOTUS] TOWNSENDII) IN WYOMING

prepared by

JEFFERY C. GRUVER¹ AND DOUGLAS A. KEINATH²

¹ Wyoming Natural Diversity Database, University of Wyoming, 1000 E. University Ave, Dept. 3381, Laramie, Wyoming 82071; 307-766-3023

² Zoology Program Manager, Wyoming Natural Diversity Database, University of Wyoming, 1000 E. University Ave, Dept. 3381, Laramie, Wyoming 82071; 307-766-3013; dkeinath@uwyo.edu



prepared for

United States Department of the Interior Bureau of Land Management Wyoming State Office Cheyenne, Wyoming

December 2003

Table of Contents

SUMMARY	3
Introduction	4
Natural History	5
Morphological Description	5
Taxonomy and Distribution	
Taxonomy	6
Distribution and Abundance	7
Population Trend	9
Habitat Requirements	
General Requirements	10
Seasonal and Life History Shifts	10
Area Requirements	10
Landscape Context	11
Movement and Activity Patterns	12
Reproduction and Survivorship	14
Breeding Phenology	
Breeding Behavior	16
Population Demographics	16
Fecundity and Survivorship	16
Life History Parameters	
Spatial Characteristics and Genetic Concerns	
Food Habits	
Community Ecology	
Predators and Competitors	
Parasites and Disease	
Symbiotic and Mutualistic Interactions	21
CONSERVATION	22
Conservation Status	
Federal Endangered Species Act	
Bureau of Land Management	
Forest Service	
State Wildlife Agencies	
Natural Heritage Ranks	
Biological Conservation Issues	
Abundance and Abundance Trends	
Distribution Trends	
Habitat Trends	
Extrinsic Threats	
Direct Anthropogenic and Natural Threats	
Indirect Anthropogenic and Natural Threats	
Targeted Areas in Wyoming	
Intrinsic Vulnerability	30

CONSERVATION ACTION	30
Existing or Future Conservation Plans	30
Conservation Elements	
Tools and Practices.	
Inventory and Monitoring	
Acoustic Surveys	
Capture Surveys	
Surveys at Hibernacula or Roost Sites	
Evaluation of Habitat Use	
Population and Habitat Management	
Captive Propagation and Reintroduction	
Information Needs	41
TABLES AND FIGURES	43
Table 1. Current federal and state status and heritage program rankings of C. townsendii ir	1
Wyoming and adjacent states	
Fig. 1. The very large ears and fleshy lump on the nose (pararhinal gland) make C. townset	ndii
distinguishable from other North American bats	
Fig. 2. Photograph of <i>C. townsendii</i> in flight	
Fig. 3. Picture of <i>C. townsendii</i> at rest but alert	
Fig. 4. Eastern big-eared bats (<i>C. rafinesquii</i>) showing ears coiled (A) and uncoiled (B) Fig. 5. Sonogram of the echolocation call of <i>C. townsendii</i> recorded by an Anabat® freque	
division detector	47
Fig. 6. Range-wide distribution of <i>C. townsendii</i>	48
Fig. 7. Range and known occurrences for <i>C. townsendii</i> in Wyoming	49
Fig. 8. Schematic of the timing of reproductive events for female C. townsendii	49
LITERATURE CITED	50
Additional References	58
APPENDIX. EXPLANATION OF RANKING CODES AND MANAGEMENT STATUS ARREVIATION	JS 59

Summary

The western subspecies of *Corynorhinus*, *C. townsendii pallescens* and *C. t. townsendii* are not currently federally listed or candidate species throughout their range. Two eastern subspecies, *C. townsendii ingens* and *C. townsendii virginianus*, are currently listed as Endangered by the U.S. Fish and Wildlife Service. Both Regions 2 and 4 of the Forest Service and the Bureau of Land Management in Wyoming and Colorado list the full species as sensitive within their jurisdictions. The Bureau of Land Management in South Dakota, Nebraska and Kansas apparently does not provide any special protection for the bats. The Wyoming Natural Diversity Database lists it as being of particular conservation concern as indicated by its S1 ranking. The state heritage ranks for *C. townsendii* in the other Rocky Mountain states range from S1 to S3 (Table 1), reflecting the rarity and vulnerability of the species in those states. The Wyoming Game and Fish Department considers *C. townsendii* to be category 2 Native Species Status (NSS2), while none of the other states neighboring Wyoming confer any special status to the bat beyond Natural Heritage ranks.

Although *C. townsendii* is found throughout most of the western United States, including British Columbia, central Mexico and the Baja Peninsula, it appears to be relatively uncommon throughout its range. *C. townsendii* is a cavernicolous species, meaning that it relies on cave-like structures for shelter during all portions of its life cycle. Though there are reports of cavernicolous species occasionally using hollows in large trees or abandoned buildings, caves and mines remain essential landscape features to *C. townsendii* and for other species of bats that use caves and mines during various stages of their life cycle. Reliable data on the abundance of *C. townsendii*, as with most species of bats, is lacking. However, there is general concurrence amongst bat biologists that there has been a downward trend in abundance of the species over the past half century. This trend is attributed primarily to renewed mining at historic sites, the closure of tens of thousands of

abandoned mines without consideration of their habitat potential, and direct and indirect disturbance by human visitors at caves and mines.

C. townsendii is particularly sensitive due to a variety of intrinsic biological factors including its habitat specificity, fragmented distribution, low reproductive rate, and intolerance of direct disturbance. The primary threats throughout the Rocky Mountain region are closure of abandoned mines, renewed mining at historical sites, recreational caving, and conversion and alteration of roosting and foraging habitat. Therefore, the primary conservation considerations are: 1) the preservation and protection of suitable maternity roosts and hibernacula, and 2) the maintenance of suitable landscape components (i.e., foraging, commuting, and drinking habitat) near these roosts.

Introduction

The goal of this document is to summarize and synthesize the relevant data on the natural history, biology and ecology of Townsend's big-eared bat (*Corynorhinus townsendii*, Cooper, 1837) with an eye toward information that would be of use to federal land management agencies in considering its conservation. This synthesis draws most heavily from the primary literature (e.g., peer-reviewed publications), but it also contains information gleaned from the gray literature (e.g., federal government technical reports, state wildlife agency and heritage program reports, university theses and dissertations, etc.) and web-based sources (e.g., NatureServe Explorer).

In some instances facts, figures, or interpretation that are presented in this document have been obtained from unpublished sources (e.g., personal communications), and are noted as such.

Interpretations based on unpublished data or personal observations represent the expert opinion of the source of the information based on their experience with the subject. Only acknowledged experts on the facts in question have been thus consulted and cited.

The information summarized in this document is derived largely from an assortment of species- and taxa-specific studies and surveys conducted across time and space. When considered collectively, these data depict the biology, ecology and natural history of *C. townsendii* across its range. However, studies and surveys are often temporally and spatially limited, and are not conducted at random locations. Accordingly, inferences drawn from these data can be tenuous, and are subject to some uncertainty.

Uncertainty also stems from potential differences in ecological responses by the various subspecies of *C. townsendii* (only *C. t. pallescens* occurs in Wyoming). Where summary and inference are based upon results from work conducted on subspecies that do not occur in Wyoming, we have noted how these results may apply to the state. However, these inferences are necessarily speculative.

Natural History

Morphological Description

Townsend's big-eared bat is a medium sized bat with overtly large ears and characteristic bilateral horseshoe-shaped lumps on the muzzle (Fig. 1), giving the bat one of its common names: the lump-nosed bat. The lumps, actually enlarged pararhinal glands, emit sebaceous secretions that are apparently involved with mating (Pearson et al. 1952, Quay 1970). The dorsal hairs are gray at the base and the tips vary from pale cinnamon to blackish brown. Ventral hairs are gray at the base, brown or buff at the tips (Kunz and Martin 1982). Length of ear and tragus are 30-39 mm and 11-17 mm respectively (Kunz and Martin 1982). The ears are erect and point slightly forward in flight (Fig. 2) and at rest (Fig. 3). However, during torpor and hibernation, the ears often are curled tightly along the head (in the shape of a ram's horn) leaving only the long pointed tragus visibly erect (Fig. 4). One or both ears may be seen coiled (Barbour and Davis 1969).

Length of the forearm ranges from 39-48 mm (Clark and Stromberg 1987). Overall length is 90-112 mm, and mass ranges from 5-13 g in adults. Females tend to be slightly larger than males (Kunz and Martin 1982). However, because size is an equivocal and unreliable diagnostic, females may be distinguished from males only upon close examination for external genitalia or the presence of mammary glands and nipples (Racey 1988). The altricial young enter the world naked with eyes closed and ears flaccid. In one study, neonates averaged 2.4 g with a forearm of 16.6 mm at birth, with no significant difference between males and females (Pearson et al. 1952).

The echolocation call of *C. townsendii* (Fig. 5) is typical of many insectivorous microchiropterans. The call is characterized by frequency modulated (FM) pulses of relatively low intensity and low duty cycle (i.e., signal on ca. 4% of the time). Bats that process returning echoes primarily in the time domain (versus bats that interpret the Doppler shift of an echo) use low duty cycle calls (i.e., high interpulse interval), thereby minimizing overlap between outgoing call and returning echoes (Gould 1970). The duration (and therefore the bandwidth) of the fundamental harmonic of the echolocation pulse is relatively short. However, *C. townsendii* makes greater use of secondary harmonics, thus increasing the effective bandwidth of the call (Fenton 1982). Broadband FM calls are effective for target detection amongst background clutter and are often correlated with a wing morphology that allows slow, highly maneuverable flight (Norberg and Rayner 1987). Indeed, *C. townsendii* has relatively broad, rounded wings resulting in low wing loading and low aspect ratio (Farney and Fleharty 1969).

Taxonomy and Distribution

Taxonomy

Townsend's big-eared bat is in the family Vespertilionidae and the tribe Plecotini, which contains the genera *Barbastella*, *Corynorhinus*, *Euderma*, *Idionycteris*, *Otonycteris*, and *Plecotus*.

Due to early uncertainty regarding the taxonomy of species and inconsistencies in nomenclature of the North American plecotine bats (*Corynorhinus, Euderma, Idionycteris,* and *Plecotus*), the systematic classification of this group has a history of flux. Kunz and Martin (1982) reported "considerable confusion in the use of the appropriate binomen for this taxon." Indeed, Townsend's big-eared bat has been referred to by three different genera (*Synotus, Plecotus,* and *Corynorhinus*) and two specific epithets (*macrotis* and *townsendii*) (Allen 1916). The use of *P. rafinesquii* in reference to *P. townsendii*, an apparent confusion at the species level, also was common before Handley's (1959) revision of New World plecotines (e.g., Pearson et al. 1952).

Cooper (1937) first described the Townsend's big-eared bat and placed it in the Old World genus *Plecotus*. On the basis of morphologic differences between members of the New and Old World species, Allen (1865) revised the taxonomic status to the newly erected genus *Corynorhinus*. Handley (1959), reviewed the taxonomic history of the plecotine group, reevaluated Townsend's big-eared bat back to the genus *Plecotus* and demoted *Corynorhinus* to subgeneric level. Two recent phylogenetic studies provided evidence to re-elevate *Corynorhinus* to generic level and differentiate *Corynorhinus* from the Old World *Plecotus* (Frost and Timm 1992; Tumlinson and Douglas 1992). Subsequently, the New World species were placed back into the genus *Corynorhinus*, and this is the currently accepted and genetically supported nomenclature (e.g., Bogdanowicz et al. 1998). The generic name *Corynorhinus*, coined by Allen (1865), is derived from the two Greek roots coryn (= a club) and rhin (= a nose), referencing the characteristic large fleshy lumps on the bat's nose.

Distribution and Abundance

Corynorhinus townsendii is geographically widespread in western North America, but tends to be locally limited by the presence of suitable roosting habitat (e.g., caves, mines, lava tubes,

abandoned buildings) (Kunz and Martin 1982). The eastern extent of the range of the western races of the big-eared bat includes the Black Hills of South Dakota and Wyoming, south-central Kansas, western Texas and Mexico. The range extends north into southern British Columbia, west into the Pacific Northwest, and south through California into the Baja peninsula and Mexico (Fig. 6). Although the range across most northern Rocky Mountain States is wide, (Fig. 7) actual distribution is relatively restricted, reflecting the eastern and northern limits of the species' range and scarcity of suitable roost sites.

Townsend's big-eared bat it is not very abundant anywhere in its range (Barbour and Davis 1969) largely due to the patchy distribution and limited availability of suitable roosting habitat. For instance, surveys at abandoned mines and caves in Colorado have revealed 14 maternity roosts, most of which contained fewer than 50 individuals (K. Navo, Colorado Division of Wildlife, pers. comm.).

Owing to their nocturnal and volant habits, reliable estimates of population densities of bats are difficult to obtain (O'Shea and Bogan 2000). Notwithstanding, Humphrey and Kunz (1976) estimated the density of big-eared bats to be one bat per 38 ha on a 46.6 km² tract in Oklahoma. Pearson et al. (1952) estimated a density of one bat per 126 ha in northern California and 1 bat per 170 ha on Santa Cruz Island off the coast of California. Because of the usual difficulties in deriving these types of estimates, Pearson et al. (1952) considered these numbers to be upper limits. Unfortunately, these estimates cannot properly be extrapolated across the species' range because they were not derived from a random sample of locations within the range. The logistical and technical difficulties associated with developing abundance estimates for bats has been treated by O'Shea and Bogan (2000) and is discussed below in Tools and Practices.

Population Trend

Reports from monitoring efforts at known nursery sites and hibernacula in the western United States indicate a long-term decline in numbers (Perkins and Levesque 1987, Pierson and Rainey 1996, O'Shea and Vaughan 1999). Continued habitat degradation, manifest as loss and disturbance of summer and winter roosting habitat (e.g., caves and mines) and alteration and removal of foraging habitat, can be expected to limit reproduction and dispersal opportunities, further impacting populations. Indeed, Pierson and Rainey (1996) concluded that populations of *C. townsendii* in California are limited by lack of suitable undisturbed roosts.

Habitat Requirements

In general, *C. townsendii* requires spacious cavern-like structures for roosting (Pierson et al. 1999) during all stages of its life-cycle (i.e., maternity roosts, day and night roosts, and hibernacula). Townsend's big-eared bat forages along edge habitats (e.g., forested edges and intermittent streams), in forested habitat and along heavily vegetated stream corridors, and in open areas near wooded habitat, though they appear to avoid open, grazed pasture land (Pierson et al. 1999). Water sources required for drinking generally must be open and accessible. Additionally, the water must be calm and fresh. Open ponds associated with mining activity, particularly gold mining, may be used by bats, but have been implicated in the deaths of bats because of heavy metal contamination (Pierson et al. 1999).

Corynorhinus bats generally use caves and mines as diurnal retreats but have been noted roosting in large hollows of redwood trees in California (Fellers and Pierson 2002), in the attics of abandoned buildings (Dalquest 1947, Fellers and Pierson 2002) and under bridges (Keeley 1998, Adam and Hayes 2000). Selection of specific structures for maternity roost or hibernacula seems to be driven by temperature, preferring hibernacula roosts that remain above freezing (or have

regions that do) and that have moderate airflow (Pearson et al. 1952, Genter 1986, Prather and Briggler 2002).

General Requirements

In Utah, big-eared bats used caves and mines at lower elevations (1350-2440 m) as maternity and bachelor roosts. These roosts were associated with sagebrush-grass steppe, juniper woodlands, and mountain brush (Sherwin et al. 2000). However, for *C. t. ingens*, a number of studies have shown that external vegetative characteristics do not seem to drive selection of cave roosts (Clark et al. 1996, Wethington et al. 1997, Prather and Briggler 2002).

Seasonal and Life History Shifts

Townsend's big-eared bat has been referred to as a cave and mine obligate because it using these structures during all parts of its life cycle. Caves and abandoned mines are used both for summer roosts and hibernacula. Individuals frequently move within and between roosts during summer and winter (Genter 1986; Sherwin et al. 2000). Available evidence suggests that *C. townsendii* uses staging roosts, to which they show little fidelity, between the dissolution of maternity colonies and arrival at hibernacula in the fall (Pearson et al. 1952) and between exodus from the hibernacula and arrival at maternity colonies in the spring (Dobkin et al. 1995). The purpose of these interim roosts is unclear, but they may serve as "staging grounds" that foster commingling of the sexes for breeding, promote synchronous arrival of pregnant females at maternity roosts, or serve to apprise juveniles of the location of hibernacula.

Area Requirements

In general, minimum areal requirements will depend on density of conspecifics and competitors, site productivity with respect to insect prey, availability of water, and average ambient temperature.

During the latter stages of reproduction (lactation and post-lactation), females of the two eastern subspecies (C. t. ingens and C. t. virginianus) appear to increase their foraging areas (Clark et al. 1993; Adam et al. 1994), apparently in order to meet the increased energetic demands of lactation or to allow newly vagile young to exploit the nearby foraging areas. Clark et al. (1993) observed a four-fold increase (1 km to 4.2 km) in median distance traveled to foraging sites by C. t. ingens between early lactation and late lactation in Oklahoma, and one female traveled more than 7 km to foraging sites during late lactation. Female C. t. virginianus in Kentucky increased their foraging areas from 60 ha to 263 ha between pregnancy and post-lactation, while males decreased their foraging areas during the same period (Adam et al. 1994). Similarly, during the post-lactation period in coastal central California (mid-September), female big-eared bats traveled 3.2 km on average to foraging sites, a distance significantly greater than the 1.3 km averaged by males during the same period (Fellers and Pierson 2002). In east-central Nevada, female C. t. pallescens were observed foraging from 0.8 to 6.4 km from their roosts in mid-August, a period that would coincide with late lactation (Bradley 1996). Post-reproductive female C. t. ingens in Oklahoma traveled shorter distances to foraging areas and used smaller foraging areas than did reproductive females (Wethington et al. 1996).

Landscape Context

Several authors (e.g., Limpens and Kapteyn 1991, Verboom and Huitema 1997, Fellers and Pierson 2002) have noted an apparent propensity for bats to use forest-edge habitat for commuting and foraging and have hypothesized that these landscape elements provide orientation cues, foraging habitat and, perhaps, shelter from predators for the bats. Adam et al. (1994) reported that male *C. t. virginianus* consistently used an abandoned logging road in Daniel Boone National Forest to commute to foraging areas in open hollows, and although females did not have access to a similar corridor, they tended to fly along the edges of cliffs en route to foraging areas.

Movement and Activity Patterns

The circannual and diurnal activity patterns of *C. townsendii* mirrors that of most other north-temperate species of bats and is dictated largely by the seasonal cycles of warm and cold and the daily cycles of light and dark. Bats of the north temperate regions of the world are regularly active only during the summer months when insects are available and warm temperatures allow efficient thermoregulation. Bats are almost exclusively nocturnal, irrespective of phylogenetic affiliation, trophic niche, or geographic location, and typically remain in seclusion during the daylight hours, often in a state of shallow torpor (Barbour and Davis 1969). Noting that there is a significant opportunity cost to not foraging during the day – namely lost foraging opportunities and concomitant reliance on torpor to balance energy budgets – Speakman (1995) reviewed three possible explanations for bat nocturnality: 1) reduced fitness from competition with diurnal competitors; 2) risk of predation by diurnal predators; and 3) risk of hyperthermia. Recognizing the paucity of available data with which to adequately evaluate the relative likelihoods of each alternative, he concluded that risk of predation was the most important factor in limiting diurnal activity in temperate-zone bats (Speakman 1995).

Unlike males and non-lactating females, who remain away from the day-roost most of the night, lactating females return to the roost between evening foraging bouts to nurse their young (e.g., Kunz 1974, Barclay 1982, Racey and Swift 1985, Adam et al. 1994, Waldien and Hayes 2001). Even though males and non-lactating females remain away from the day-roost most of the night they are not active all night long. Many species of bats use night-roosts to rest and digest food, and night-roosts may serve social functions (Perlmeter 1995). Night-roosts are used during all stages of reproduction (Lacki et al. 1994, Perlmeter 1995, Adam and Hayes 2000), though lactating females use them to a lesser degree (Barclay 1982). Night-roosts often harbor multiple species (Dalquest 1947, Perlmeter 1995).

Foraging activity at any particular place can be quite variable across time (Hayes 1997). This variability likely reflects the ephemeral and patchily distributed nature of insect populations, as well as variation in local weather conditions (e.g., wind, precipitation, temperature) that alter the energetic costs associated with foraging and thermoregulation. Paige (1995) suggested that the ability of cave-roosting pipistrelles to track barometric pressure, a good predictor of insect abundance, might inform decisions regarding the benefits of foraging versus remaining at the roost. Despite the evolutionary implications of such a strategy, this line of inquiry seems to have received little attention from researchers.

Moon phase is another mechanism thought to be responsible for changes in bat's daily activity patterns. It has long been held that bats are lunaphobic. This belief was based on the anecdotal evidence that capture success during bright moonlit nights tended to be lower than during overcast nights or nights with little moonlight. Hypotheses to account for the putative lunaphobic behavior relate to increased predation risks to bats that were active on bright nights and/or decrease in abundance of insect prey (e.g., Reith 1982, Anthony et al. 1991, Hecker and Brigham 1999). Evidence suggests that activity levels for most north-temperate insectivorous bats are not correlated with lunar phase or ambient light levels (Karlsson et al. 2002), although results seem to be time and space dependent and the phenomenon apparently is widespread amongst neotropical species (Morrison 1978; Usman et al. 1980). Foraging activity of *C. t. virginianus* has been shown to be negatively correlated with moon phase (Adam et al. 1994), but moon brightness did not affect flight activity in *C. t. ingens* (Clark 1991).

As with many other nearctic species of bats, *C. townsendii* escapes the harsh conditions and lack of prey during winter by hibernating. Dissolution of maternity colonies and movements toward hibernacula begin in late summer after juveniles are fully weaned and volant (Pearson et al.

1952). By October, big-eared bats begin to arrive at hibernacula, and maximum numbers are present in January (Pierson et al. 1999). Western big-eared bats are relatively sedentary species, and appear not to engage in long distance migrations to hibernacula. Maximum recorded distances moved are 40 km for western big-eared bats (Humphrey and Kunz 1976) and 64 km for eastern big-eared bats (Barbour and Davis 1969).

Reproduction and Survivorship

Relative to other mammals, bats display remarkable flexibility in the reproductive cycle, particularly in north-temperate regions where reproductive delays are common. Three general categories of reproductive delay are recognized in bats: delayed fertilization, delayed implantation, and delayed development (Racey and Entwhistle 2000). Delayed fertilization is the most widespread strategy used by nearctic species of bats and is associated with prolonged storage and survival of sperm in the female reproductive tract (Racey and Entwhistle 2000). For species that employ delayed fertilization, ovulation occurs upon arousal from hibernation in the spring, and the reproductive cycle continues normally (Racey and Entwhistle 2000). The most complete analysis of breeding biology and behavior of *C. townsendii* to date was conducted by Pearson et al. (1952) for bats in northern California. Except where otherwise noted, the information on breeding that follows is summarized from their work.

Like all insectivorous bats of north-temperate regions, *C. townsendii* is seasonally monoestrous (Racey and Entwhistle 2000). Breeding behavior is most vigorous in autumn (but copulation may also take place sporadically through the winter) and parturition occurs during the summer months (Fig. 8). Being subject to the physiological constraints of hibernation, females suspend normal progression of the reproductive cycle (i.e., ovulation, fertilization, implantation, and gestation) between copulation and parturition (Neuweiler 2000), the precise physiological

mechanisms for which remain largely unknown. This discontinuity in the reproductive cycle is hypothesized to synchronize parturition to periods of optimal food resources and developmental conditions for the young (Racey 1979).

Breeding Phenology

Initiation of sperm production in adult males begins in the spring and continues slowly until late summer when there is a rapid increase in the size and volume of the accessory glands.

Juvenile males produce sperm, albeit in small numbers, which apparently do not migrate into the epididymides. Thus, males are effectively sterile until their second year.

Females enter estrous in late summer or early fall, at which time they are sexually receptive.

Copulation commences during this time as the sexes converge on winter hibernacula. Although coitus primarily occurs in the hibernacula, many females, including young of the year, are mated before arriving at the hibernacula in late October. Mating continues throughout hibernation during periods of arousal from torpor.

Upon arousal from hibernation in the spring, females that have been mated ovulate and the reproductive cycle continues uninterrupted. The length of gestation varies from 40 to 60 days and is apparently dependent on ambient temperature (Kunz and Martin 1982) and precipitation (Grindal et al. 1992). When post-arousal temperatures are low and precipitation is high, bats face higher thermoregulatory costs and lower prey availability, resulting in increased use of torpor and concomitant delays in development of the fetus.

Parturition occurs later in yearling females than in adults, but in general, timing seems to be unrelated to latitude. Parturition began in late May in California, mid-July in Washington state, and June in Texas (Kunz and Martin 1982). Juveniles are capable of flight about 3 weeks after parturition, but continue to receive milk up to 6 weeks following birth.

Breeding Behavior

Although males appear to be largely responsible for initiation of the reproductive process, once the hibernation period ends and the bats disperse, males are completely dissociated from the process. Males play no role in the rearing of the young, and are rarely present in the roosts of pregnant and lactating females (Kunz and Martin 1982).

In general, males mate with multiple females, and females are inseminated by multiple males. The male initiates pre-copulatory behavior by approaching a pendant female from the front while vocalizing ("making twittering sounds") and embracing her. For a period of some minutes during the embrace, the male fervently rubs his snout over the face, neck, forearms and ventral surface of the female. This behavior was assumed to involve the enlarged nose glands (Fig 1) and was interpreted to be an attempt to encourage capitulation of the female. In the one instance during which this behavior was observed in the lab by Pearson et al. (1952), the male attempted to mount the adult female from the rear, but she was apparently uninterested in the advances of the male despite her unmated condition, as she attempted escape and flew short distances. The male searched for her and initiated the same behaviors on the first bat (male and female, torpid and not) that he happened upon. For copulations observed or inferred by Pearson et al. (1952) in the wild, the females were torpid, which, when considered along with the behavior of what should have been a receptive female in the lab, suggests that females are a passive part of the copulatory process.

Population Demographics

Fecundity and Survivorship

Females typically give birth to a maximum of 1 young per year. It is unknown whether females forgo reproduction in some years as a result of resource limitations. Mortality of juveniles is estimated to be 38-54% (Pearson et al. 1952). Some of that mortality may be

attributable to insufficient fat reserves to make it through hibernation, as survival rates are about 80% in succeeding years (Pearson et al. 1952). However, because there were relatively few young bats present in hibernacula, Pearson et al. (1952) speculated that most juvenile mortality occurred prior to the bats entering hibernation. Paradiso and Greenhall (1967) recorded an age of 16 years 5 months for an individual *C. townsendii* in California. More recently, a new longevity record of over 21 years for *C. townsendii* was established (Perkins 1994).

Life History Parameters

Nocturnality is a characteristic trait of bats and has played an important role in the evolution of life histories of bats (Barclay and Harder 2003). Speakman (1995) provided an exegesis of the most commonly evoked hypotheses for nocturnality in bats: 1) risk of avian predation; 2) increased competition with diurnal insectivorous birds; and 3) risk of hyperthermia from exogenous daytime heat load. He concluded that, given available information, no single factor adequately explained chiropteran nocturnality. However, at certain sites, predation and hyperthermia appeared to be plausible explanations, whereas competition with diurnal insectivores seemed least likely.

As a group, bats live longer and have lower reproductive output than would be predicted for mammals of their size, or for similarly sized terrestrial mammals (Barclay and Harder 2003). For instance, many nearctic species of bats may live upwards of a decade and give birth once per year to one or two pups. One of the consequences of this low reproductive rate is that populations that experience rapid declines may be unable to replenish their numbers in the absence of immigration. This is a particular concern for species such as *C. townsendii* that are sedentary and exhibit a high degree of site fidelity (Kunz and Martin 1982).

Spatial Characteristics and Genetic Concerns

Townsend's big-eared bats are a sedentary species that are not known to engage in long-distance migrations (Kunz and Martin 1982), and for which mating occurs at winter hibernacula (Pearson et al. 1952). Therefore, it is unlikely that there is much gene flow between populations. As well, the distribution of *C. townsendii* tends to be restricted by the presence of caves and mines that are not distributed uniformly across the landscape, and are separated by patches of unsuitable habitat. This scenario suggests the appropriateness of a metapopulation model to depict the overall population of the species.

Food Habits

Based on the morphology of the wings and echolocation, which allow slow maneuverable flight and target discrimination amongst background clutter respectively, bats in the genus *Corynorhinus* are predicted to be able to efficiently forage amongst foliage or glean insects directly from substrates. All reports indicate that *C. townsendii* is a moth specialist (Whitaker et al. 1977, Clark 1991, Burford and Lacki 1998, Pierson et al. 1999). Like other species of bats, *C. townsendii* probably forages opportunistically, and small quantities of Coleoptera and Diptera, and representatives of various other orders, are often found during studies of diet (Pierson et al. 1999).

Community Ecology

Most species of bats exhibit life histories characteristic of K-selected species (Findley 1993). Therefore, it seems unlikely that predation has played a very large role in the evolution of their life histories, nor, by extension, in shaping their communities. By virtue of their nocturnality bats avoid direct competition for food with diurnal insectivorous birds. Yet bats have not completely escaped these two pressures. Predators sometimes take bats opportunistically, while the bat hawk (*Machaerhampus alcinus*) of Africa feeds nearly exclusively on bats (Hill and Smith 1984).

More important from the perspective of community ecology is competition with conspecifics, which likely influences community structure and dynamics. North temperate bat communities appear to be saturated (sensu Findley 1993), suggesting that competition is an important factor in structuring bat communities. However, the extent to which competition drives the structure of these assemblages remains equivocal (Findley 1993, Kingston et al. 2000). Patterns in the structure of local bat assemblages often are suggestive of resource partitioning (e.g., Aldridge 1986, Aldridge and Rautenbach 1987, Crome and Richards 1988), but there is little direct evidence of competition.

Predators and Competitors

The bat hawk (*Machaerhamphus alcinus*) of Malaysia, New Guinea, and sub-saharan Africa is the only animal known to regularly include bats in the diet. However, snakes, birds, and mammals have been reported to prey on bats opportunistically (Barbour and Davis 1969, Fenton et al. 1994), particularly those species of bats that roost in very large aggregations (e.g., *Tadarida brasiliensis*). Owing to its colonial and visible roosting habits, *C. townsendii* may be more susceptible to predation than some other bats.

Reports of predation on *C. townsendii* include a gopher snake (*Pituophis melanoleucus* catenifer) with a juvenile big-eared bat in its mouth (Galen and Bohn 1979), and cats and raccoons preying on *C. townsendii* as the bats emerged from caves (Tuttle 1977, Bagley 1984, Bagley and Jacobs 1985). Fellers (2000) provided circumstantial evidence of predation by the black rat (*Rattus rattus*) on juvenile big-eared bats in an attic roost. The common thread in these accounts is that the bats were concentrated spatiotemporally either at the roost or as they emerged from the roost – a scenario wherein opportunistic attacks are likely to be most fruitful for the predator.

Although several reports have documented the presence of bat remains in owl pellets (Krzanowski

1973, Doggart et al. 1999, Love et al. 2000), the extent of depredation by nocturnal avian predators on foraging or commuting bats – which are more spatially dispersed across the landscape – remains largely unknown, perhaps owing to the difficulty in witnessing such events.

No studies have attempted to directly assess competitive interactions between Townsend's bigeared bat and other species of bats, and there is some question as to whether bat communities are regulated by competition for resources (Findley 1993). However, evidence for competition between sympatric species of bats comes from examination of community structure. For instance, Husar (1976) demonstrated disparate diets for morphologically similar species of *Myotis* where they co-occurred and overlap in diets where they were allopatric, strongly suggesting behavioral resource partitioning. Similarly, Arlettaz (1999) demonstrated segregation of space and prey items between two sympatric species in the genus *Myotis*. This type of evidence, along with species-specific morphology and behaviors, suggests strategies designed to minimize direct competition with congeners or confamilial bats. Similarly, variation in wing and echolocation morphologies in bats have been correlated with different foraging styles (e.g., fast, aerial hawking vs. slow, gleaning/hawking) and different foraging habitat (e.g., Aldridge and Rautenbach 1987).

Further evidence for competition among sympatric species of bats comes from the observation that different species seem to emerge to forage at different, and often predictable times (Jones 1965; Barbour and Davis 1969; Fenton et al. 1980), a behavior that may represent temporal partitioning of the same resource. An acute example of this is provided in Kunz's (1982) review of *Lasionycteris noctivagans*, in which he marshals evidence from Kunz (1973), Whitaker et al. (1977) and Reith (1980), to show that *L. noctivagans* alters its activity period when sympatric with the ecologically similar species *Lasiurus borealis*, *L. cinereus*, and *Eptesicus fuscus*.

Parasites and Disease

A number of external parasites are known to complete all or part of their life cycles on bats. In California, two species of fleas (*Nycteridopsylla vancouverensis* and *Myodopsylla palposa*) were identified from Townsend's big-eared bats (Haas et al. 1983). However, none of these parasites are thought to deleteriously effect populations. Lewis (1995) hypothesized that reduction of parasite loads should increase fitness and may explain part of the costs associated with frequent roost switching behavior. If so, roost switching by *C. townsendii* may be attributable partially to efforts to manage parasite loads.

As with all mammals, *C. townsendii* is susceptible to the rabies virus. However, the prevalence of the disease in natural populations of bats appears to be exceedingly low – one study reported the incidence to be less than 0.5 % (Constantine 1979) – and probably does not play a significant role in the population dynamics of bats. West Nile virus has been confirmed in bats from a small number of cases in the United States. However, the degree to which bats are exposed to the virus and its population-level effects are currently unknown.

Symbiotic and Mutualistic Interactions

Although *C. townsendii* is known to share roosts with other species of bats, no hypotheses regarding mutual benefits have been proposed. Likewise no symbiotic or mutualistic relationships are known between *C. townsendii* and extra-ordinal species.

Conservation

Conservation Status¹

Federal Endangered Species Act

Two of the four subspecies found in the U.S. (*C. t. ingens* and *C. t. virginianus*) have been listed as endangered by the U.S. Fish and Wildlife Service since 1979 (USFWS 1979). The two western subspecies (*C. t. pallescens* and *C. t. townsendii*) are currently considered sensitive or species of concern throughout their range (Pierson et al. 1999).

Bureau of Land Management

The BLM in Wyoming considers *C. townsendii* a Sensitive species as defined: "(1) a species under status review by the FWS/National Marine and Fisheries Service (NMFS); or (2) a species whose numbers are declining so rapidly that Federal listing may become necessary; or (3) a species with typically small or widely dispersed populations; or (4) those species inhabiting ecological refugia or other specialized or unique habitats." (BLM Wyoming 2001). The BLM in Colorado also considers *C. townsendii* to be a Sensitive Species.

Forest Service

Region 2 of the US Forest Service ranks *C. townsendii* as a Sensitive species. For the Forest Service, Sensitive species are: "those plant and animal species identified by the Regional Forester for which population viability is a concern as evidenced by: a) significant current or predicated downward trends in population numbers or density, or b) significant current or predicated downward trends in habitat capability that would reduce a species' existing distribution" (USDA Forest Service 1994).

¹ See Appendix for a complete description of management status abbreviations

State Wildlife Agencies

The Wyoming Game and Fish Department (WGFD) assigns *C. townsendii* a state special concern rank of NSS2 (Native Species Status 2). The NSS2 rank is based on WGFD estimates that populations in Wyoming are restricted in numbers and experiencing ongoing significant loss of habitat, although extirpation is not deemed imminent (Oakleaf et al. 2002). WGFD ranks native species on a scale of NSS1 to NSS7, with NSS1 representing critically imperiled species and NSS7 representing stable or increasing species. These ranks are assigned by WGFD biologists as a way to roughly prioritize wildlife concerns in the state, but they carry no legal, regulatory, or management weight per se.

Natural Heritage Ranks

NatureServe, the association of Natural Heritage organizations, ranks species' status across their range (referred to as G ranks or Global Ranks). Each state or province ranks a species' status within its own geopolitical boundaries (referred to as S ranks; Table 1). The two western subspecies (*C. t. pallescens* and *C. t. townsendii*) are regarded as G4 species (NatureServe Explorer 2001), signifying that they are "apparently secure, although the species may be quite rare in parts of its range, especially at the periphery" (Fertig and Heidel 2002). 25 western states and provinces have assigned a State Rank to *C. townsendii* at the species level, and 14 of these states rank it as S2 (imperiled) or S1 (critically imperiled). In general, state ranks are assigned based on the assessed risk of extinction within a state, where S1 species are deemed critically imperiled and S5 species are deemed demonstrably secure. These assessments are based on biological information on population status, natural history, and threats at the state level. Specific State Ranks are as follows: Arizona (S3), Arkansas (S1), British Columbia (S2S3), California (S3S4), Colorado (S2), Idaho (S2?), Kansas (S2), Kentucky (S1), Missouri (SX - extirpated), Montana (S2S3), Navajo Nation (S3), Nebraska (S1), Nevada (S3B), New Mexico (S3), North Carolina

(S1), Oklahoma (S3), Oregon (S3), South, arolina (S1), South Dakota (S2S3), Texas (S3?), Utah (S3S4), Virginia (S1), Washington (S2S3), West Virginia (SU), Wyoming (S1B,S2N).

Biological Conservation Issues

We have divided the discussion of conservation issues into biological conservation status, extrinsic threats and intrinsic vulnerability. Biological status synthesizes some of the key parameters noted earlier in this document, and the other two categories represent factors that impact populations and thus result in this status. Intrinsic factors include those things driven primarily by the biology of the species, such as lifespan and reproductive rate, while extrinsic factors are driven by external forces, such as depredation, habitat loss, habitat disturbance, and reduction of prey base. The section concludes with a discussion of specific management implications and the tools and practices that might be used to facilitate conservation of the species.

Abundance and Abundance Trends

Noting that *C. townsendii* had taken advantage of anthropogenically created roosting habitat (e.g., abandoned mines and buildings), Pearson et al. (1952) suggested the potential for an increase in abundance of these bats. Yet, western populations of *C. townsendii* have declined markedly over the past 40 years (Perkins and Levesque 1987, Pierson and Rainey 1996, O'Shea and Vaughan 1999). One potential explanation for the observed decline is that roosting habitat is actually decreasing. Indeed, Meier and Garcia (2001) estimated that 32,738 mine portals have been closed since ratification of the Surface Mining Control and Reclamation Act of 1977, and the average number of closures per year has been increasing. During the first six years of the Act, an average of 785 portals were closed per year, but for the biennium ending in September 2000, closures averaged 2813 per year (Meier and Garcia 2001). Another explanation is that an increase in the quantity of roosting habitat may not automatically lead to an increase in numbers of bats. Altenbach and Sherwin (2002), speculating on the potential results of increased roosting habitat in the form of abandoned mines on the distribution and abundance of cave-dwelling species of bats,

proposed that, if density-independent mechanisms (e.g., energetic constraints) regulated abundance of cavernicolous bats, then an increase in roosting habitat may serve to distribute bats more evenly in space but would not necessarily result in increased numbers of bats. In support of this hypothesis, they cite the smaller and more evenly distributed colonies residing in mines relative to colonies in caves, and the decrease in colony size in mines as distance to portions of the range where caves occur increases.

Distribution Trends

For a cavernicolous species such as *C. townsendii*, the creation of man-made roosting habitat (i.e., mines) certainly has (or has had) the potential to increase the distribution of the species (Pearson et al. 1952). However, lacking concise data on the historic distribution of *C. townsendii*, it is difficult, if not impossible, to adequately assess trends in the species' distribution. As well, recently conducted surveys for *C. townsendii* have occurred mainly at sites identified as having high priority (e.g., those associated with abandoned mine lands projects) and thus have not been designed to assess distribution trends. Notwithstanding, available evidence suggests that some sites that were known to have been occupied in the past no longer harbor big-eared bats (Perkins and Levesque 1987, Pierson and Rainey 1996, O'Shea and Vaughan 1999, Pierson et al. 1999).

Range-wide, and perhaps regionally, the distribution of *C. townsendii* appears to be limited by availability of suitable roosting structures. However, at the local scale, other factors probably influence the distribution of Townsend's big-eared bat. For instance, Geluso (1978) supposed that the creation of man-made watering holes may allow local expansion of the range of *C. townsendii*. Geluso (1978) showed that *C. townsendii* is incapable of producing highly concentrated urine and, thus, is more reliant on exogenous water to maintain daily water balance than other small

insectivores. Despite this, *C. townsendii* is often associated with xeric habitats in the west and is frequently sympatric with species whose urine concentrating abilities surpass their own.

Therefore, in the absence of another mechanism for acquisition of water, *C. townsendii* distribution may be limited locally to areas with reliable, accessible sources of drinking water.

Habitat Trends

Recognition of the value of abandoned mines and caves to *C. townsendii* (Altenbach and Sherwin 2002) has somewhat increased efforts to identify and protect such roosting structures (Belwood and Waugh 1991, Altenbach 1998), probably leading to a greater distribution of potential roosting habitat for *C. townsendii* relative to unmitigated closure of abandoned mines and lack of protection at caves known to be used by the species. At the same time, however, renewed mining activities at historic sites has likely rendered unsuitable some previously used sites (Pierson et al. 1999). Thus, in the absence of baseline data on habitat availability for bigeared bats and the non-trivial efforts required to locate, survey and monitor potentially suitable cave and mine roosting habitat, there is no clear evidence on trends with regard to roosting habitat.

Pesticide spraying, conversion of native shrub-steppe to grasslands, reduction and conversion of riparian habitats as a result of livestock grazing, and timber harvest have all been implicated in a general downward trend in foraging habitat for *C. townsendii* (Pierson et al. 1999).

Extrinsic Threats

Direct Anthropogenic and Natural Threats

Natural extrinsic threats to big-eared bats consist primarily of predators (reviewed above in Competition and Predators). However, a number of direct anthropogenic threats to bats have been identified.

Because of their long residence time in the environment and bioaccumulation in the food-chain, organochlorine pesticides and their residues probably have contributed to local or regional declines of bat populations (Clark 1988*a*, Clark and Shore 2001). Although studies suggest that bats are not deficient in micosomal enzymes that detoxify xenobiotics and do not appear to be more sensitive to xenobiotics than other mammals (Clark 1988*b*), the renowned longevity and high metabolic rates of bats suggest that accumulation of residues within individuals or populations is likely. Bats – particularly small insectivorous species – may be especially susceptible in the short-term to exposure to organochlorines because they are lipophilic and concentrate in fat. Bats that must migrate or hibernate rely on fat stores and thus risk mobilizing accumulated residues. Organochlorines and their residues also concentrate in milk, and young may ingest high doses while nursing (Clark 1988*a*). Concentrations of DDE (the primary metabolite of DDT) in juvenile gray bats were found to be 2 orders of magnitude greater (0.28 mg kg⁻¹ vs. 34 mg kg⁻¹) than in juvenile birds from the same area (Clark et al. 1988). These juvenile bats also contained residue of DDD and DDT not found in the birds.

Specific LD₅₀ values for organochlorines have been difficult to assay because of the lipophilic nature of the compounds. Early dosing studies indicated that LD₅₀ values vary directly with fat levels (Clark 1988a). However, the percentage of the brain that is fat remains relatively constant regardless of fluctuations in body fat. Because the concentration of residues in brain lipids are highly correlated with that in carcass lipids once threshold concentrations are met, mean lethal concentrations have been reliably measured from brain lipids (Clark 1981 & 1988b).

Effects on reproduction of organochlorines and other toxicants has been little studied. Studies of Mexican free-tailed bats (Reidinger 1972, Clark et al. 1975, Theis and McBee 1994), big brown bats (Clark and Lamont 1976), and little brown bats (Clark and Krynitsky 1978) have shown that

DDE and DDT was present in newborns indicating that these chemicals crossed the placenta. However, the primary means of transfer is through lactation. Circumstantial evidence suggests that accumulation of organochlorine pesticide residues causes disproportionate mortality in males, and that DDE may have androgen blocking effects that can lead to interference with sexual development and fertility in males (Clark 1988a). If so, then the possibility of effects at the population level exists.

Direct application of pesticides to bats or bats roosts (e.g., Humphrey and Cope 1976) as a control method clearly has population-level effects. Clark (1988a) provides three examples of effects on populations of bats directly attributable to insecticide residue transfer and accumulation. In central Missouri, endangered gray bats (*M. sodalis*) were extirpated from one cave and numbers in nearby caves dropped in the years following application of the chlorinated insecticides aldrin and heptachlor epoxide. Dead bats recovered from the caves contained lethal levels of aldrin, its highly toxic metabolite dieldrin, and heptachlor epoxide. Recent surveys indicate that numbers of bats are returning to normal levels and that although residues are still detectable in the environment, concentrations are relatively low. In these and other cases, levels of organochlorines in guano was detectable and analysis of guano samples can be used as a "litmus test" to indicate if more detailed analysis is warranted.

In areas of Arizona, California and Nevada, where open-pit cyanide-extraction gold mining is common, bats were the most commonly recovered group of mammals found dead near the mining operations. The death of the bats was attributed to poisoning that likely resulted from drinking from the cyanide ponds (Clark and Holthem 1991).

Indirect Anthropogenic and Natural Threats

Studies to assess the impact of the bacterial pesticide *Bacillus thurengiensis* (Bt) on nontarget lepidopteran species and on foraging behavior by bats indicate that significant decreases in nontarget lepidopterans (Miller 1992). Because a significant proportion of the diet of *C. townsendii* comprises lepidopterans (Whitaker et al. 1977, Burford and Lacki 1998), activities that reduce the abundance of moths can negatively impact Townsend's big-eared bat.

Amateur recreationalists and vandals have reduced the utility of many caves and mines to bats through increased disturbance or arrant destruction (Barbour and Davis 1969). Graham (1966) documented the abandonment of a nursery colony of *C. townsendii* in California in the wake of increased visits to the site by recreationalists. Further, closures of abandoned mines in the interest of public safety has probably destroyed numerous hibernacula and/or maternity roosts. Increased awareness of mines as critical bat habitat has led to increased efforts to identify known roosts and pursue alternate closure methods (e.g., gates) that permit use by bats but minimize access by people.

Targeted Areas in Wyoming

Townsend's big-eared bat is heavily reliant on structures that provide relatively large cavernous undisturbed roosting opportunities such as caves, abandoned mines, and to a lesser degree, abandoned buildings. Therefore, management efforts focused on the identification and protection of caves and mines, particularly those in close proximity to foraging and drinking habitat, should pay the largest conservation dividends. Since these sites are so limiting, priority areas should include all currently known roosts, to include hibernacula, maternity roosts and bachelor colonies, as well as areas that contain suitable habitat (i.e., caves and mines proximate to suitable foraging and drinking habitat), but for which presence of *C. townsendii* is currently unknown.

Intrinsic Vulnerability

Townsend's big-eared bat, like most insectivorous bats, is a long-lived slowly reproducing species, and is limited to, at most, one pup per female per year. As such, populations are probably unable to recover quickly from declines.

C. townsendii utilizes deep torpor (i.e., hibernation) during the winter, and shallow torpor during the reproductive season. Individuals are especially vulnerable to predation and disturbance during these times (Thomas 1995). Any disturbance during hibernation may cause bats to utilize up to 68 days worth of crucial fat reserves as they re-warm themselves (Thomas et al. 1990).

For species with a high degree of site fidelity, such as *C. townsendii*, the importance of individual sites to population persistence increases, making such species more vulnerable than those that switch sites readily (Lewis 1995). The fragmented nature of the population (e.g., reliance on localized roost structures) increases vulnerability by increasing the likelihood of local extinctions and decreasing the potential for re-colonization of extirpated habitat. Similarly, reliance on specific habitat features (e.g., caves and mines, water holes, thermal regimes, etc.) limits potential distribution and increases the likelihood of substantial population-level impacts from climate change, disturbance and habitat alteration.

Conservation Action

Existing or Future Conservation Plans

Population declines coupled with (or perhaps because of) ongoing loss of suitable maternity roost sites and hibernacula have prompted a number of western states to develop conservation strategies for Townsend's big-eared bat. In 2002, the Nevada Bat Working Group (a subcommittee of the Western Bat Working Group) developed a conservation plan for the bats of

Nevada, including *C. townsendii*, the stated goal of which is to be a "dynamic model for the conservation of Nevada's bat fauna far into the next decade." (Altenbach et al. 2002)

Idaho recently completed a management plan for *C. townsendii* aimed at identifying, protecting and restoring viable populations of *C. townsendii* and its habitat (Pierson et al. 1999). The Western Association of Fish and Wildlife Agencies (WAFWA) has endorsed and adopted this conservation plan for *C. townsendii* (Vicki Herron, Wyoming BLM, pers. comm.). States and Provinces represented by WAFWA include: Alberta, Arizona, British Columbia, California, Colorado, Idaho, Montana, Nevada, New Mexico, North Dakota, Oregon, South Dakota, Utah, Washington, and Wyoming.

In addition to these, the International Union for Conservation of Nature and Natural Resources (IUCN) released a broad review of conservation priorities for microchiropterans (Hutson et al. 2001). The IUCN report emphasized the need to adequately protect important roost sites and local foraging habitat for *C. townsendii*.

Conservation Elements

Conservation strategies for any species should be most successful when built upon the most complete and accurate information about the species' distribution, abundance, biology, and ecology. Our understanding of the distribution and abundance, and hence population status, of big-eared bats has arguably increased over the past decade or so, but gaps remain to be filled. Therefore, continued efforts to survey caves and mines, compile and compare species inventories, and establish and maintain monitoring programs will allow resource managers to prioritize and refine conservation plans. Likewise, as our insight into the species' biology and ecology deepens, management of physical habitat features that are important to big-eared bats should be more

productive. Together, a firm grasp on both the population status and ecological requirements and responses of big-eared bats will allow proactive, flexible management.

Tools and Practices

Ouantifying ecological responses by bats presents several unique challenges to researchers. Bats tend to occur in relatively small densities over relatively large spatial scales, are highly mobile, and are not readily observable when they are most active (i.e., during nightly foraging bouts and seasonal movements). For example, assessing landscape-scale movements is problematic for most species of bats because of their small size and nocturnal and volant lifestyle, which makes tracking individuals or species during nightly foraging bouts or seasonal movements difficult. The recent advent of small portable "bat-detectors" and lightweight radio-transmitters has lowered some of these hurdles, but has not completely removed them. Additionally, most current methods of sampling active bats violate many of the assumptions required to derive rigorous estimates of population density. For instance, some species of bats (e.g., C. townsendii) are adept at detecting and avoiding mist-nets, and once captured in mist-nets, most species of bats are not easily recaptured. Therefore, estimates of density are most readily derived from surveys of populations that roost colonially in large numbers during all or part of the year (e.g., the Mexican free-tailed bat, Tadarida brasiliensis). C. townsendii forms maternity colonies and overwinters in groups, which facilitates monitoring of their populations. However, extreme caution must be used do to their extreme sensitivity to disturbance (monitoring activities could lead to roost abandonment or low natal recruitment). This sensitivity must be carefully considered in reviewing all the tools and practices noted below

Inventory and Monitoring

Three main methods are used to survey bats: capture surveys, acoustic surveys, and visual counts. Although all sampling methods have biases, those associated with acoustic and capture surveys of bats are such that estimating them is often impossible. For instance, we can be fairly certain that capture and detection surveys also do not sample all groups consistently, but we are unable to quantify the degree to which this occurs. These biases lower overall confidence in the results because they produce variation in results that cannot be accounted for.

Results of surveys to determine species presence and abundance represent a sample of bats that are active in a given area at a given time. Valid statistical inference to the larger population relies heavily on two assumptions: 1) that captures/detections represent random samples of the population of interest, and 2) that capture/detection rates do not vary across species, between sexes, or by age. There is little question that these assumptions do not hold when conducting surveys for bats. For instance, species that are adept at avoiding nets and species that tend to forage above the height of the nets may be underrepresented in results of capture surveys.

Similarly, detectors are more likely to demonstrate the presence of those species that echolocate loudly and, when detectors are deployed at ground-level, those that fly relatively close to the ground. However, we currently are unable to quantify with certainty the probability with which these subpopulations are detected because the degree to which individual bats or different species of bats vary their use of vertical space remains largely unknown (but see McCracken et al. 1997, Hecker and Brigham 1999, Kalcounis et al. 1999, and Hayes and Gruver 2000).

Townsend's big-eared bat is an example of a species that may not be sampled effectively with capture techniques because it is a slow-flying, highly maneuverable species that seems to be adept at avoiding standard capture devices. Thus, it may be underrepresented in results from surveys

that rely on captures away from roosts. Likewise, the probability of acoustically detecting *C*. *townsendii* when it is present is currently unknown. Visual counts may produce the least variable results because they are repeatable (for hibernacula) and can be accomplished using electronic means (for hibernacula or exit counts).

Acoustic Surveys

All insectivorous bats rely on echolocation while foraging and commuting. Commercially available ultrasonic "bat-detectors," are potentially valuable tools for the study of bat distributions (Gannon and Bogdanowicz 2000). Bat-detectors typically are used to determine which species are present and/or estimate the relative levels of activity in particular habitats. Detectors can be tunable narrow-band, divide-by-n broadband, or time expansion broadband models. Narrow-band detectors record only specific frequencies and thus may not be appropriate for investigating species presence or abundance. Time-expansion detectors record a wide range of frequencies and retain call characteristics important for species discrimination (e.g., harmonics, intensity, etc.), but will not record incoming calls while processing a previously recorded call. Therefore, there is some loss of information about activity levels. Broadband divide-by-n (also called frequency division) detectors record a wide range of frequencies in real time, and thus are a frequently used tool for assessing bat activity at different sites. However, species identification based on calls from divide-by-n detectors can be problematic because certain parameters of bat calls are lost, or cannot be recorded, with this type of detector. In addition, they may be generally less sensitive in detecting calls than other, albeit more expensive, detectors (Fenton et al. 2001). The efficacy of identifying species based on their echolocation calls, particularly calls recorded with one of the commercially available frequency-division detectors, is the subject of healthy debate (e.g., see Barclay 1999, O'Farrell and Gannon 1999, O'Farrell et al. 1999, and Fenton et al. 2001).

One dimension of echolocation calls often missed by frequency-division detectors is harmonics. Many bats use multiple harmonics as part of their echolocation calls, but frequency-division detectors generally only display the dominant one (Fenton et al. 2001). However, even when using frequency-division detectors, the presence of both fundamental and secondary harmonics of the echolocation calls produced by *C. townsendii* can be sometimes be seen, thus making identification easier. Their drawbacks notwithstanding, frequency-division detectors enjoy widespread use, and when used within their limits, provide reliable data about bat activity.

Capture Surveys

Mist-nets have been used to capture bats since the 1950s, and remain the most commonly employed capture method for bats. Nets vary in mesh size, can reach 18 m in length and are 2-3 m tall when fully expanded. Nets generally are erected over bodies of water (e.g., streams, ponds), across forest trails, at roost exits, or in other areas that concentrate bat activity. The popularity of mist-nets as capture devices are related to their light weight, ease of deployment, and large areal coverage relative to other capture devices. Among the disadvantages of mist-nets are that they do not capture all bats equally. Some species, particularly slower-flying and highly maneuverable species such as *C. townsendii*, seem to be apt at detecting and avoiding mist-nets and as a result, these species may consistently be underrepresented by capture surveys.

Harp traps (Tuttle 1974) consist of a double box frame through which fine wires (often monofilament line) are strung. Bats that fly into the wires drop into a heavy canvas bag suspended from the base of the frames. A sheet of heavy plastic can be hung from the insides of the bag to prevent escape of bats that crawl up the sides of bag. Kunz and Kurta (1988) provide illustrations and recommendations for the placement of harp traps. In general, the effective use of harp traps is restricted to situations where the flight of bats is (or can be made to be) spatially constricted (e.g., cave or mine exits, building exits). As with other sampling methods, species-specific differences

likely exist in capture rates with harp traps. However, whether this bias is real and the degree to which it occurs is unknown.

Surveys at Hibernacula or Roost Sites

Surveys conducted routinely at hibernacula may provide reliable information on long-term population trends because hibernacula tend to be relatively permanent and accommodate sizeable numbers of bats (Thomas and LaVal 1988). However, due to the sensitivity of hibernating bats to human intrusion (Thomas 1995, Speakman et al. 1991), recommendations for survey frequency in hibernacula range from annual to bi-annual. Navo (1994 &1995) and Altenbach and Milford (1995) describe methods and timing for surveys for bats at mines.

When the locations of summer or maternity roosts are known, emerging bats may be sampled non-intrusively by stationing observers at roost exits to count numbers of individuals or by placing electronic counting devices near roost exits (Bagley and Jacobs 1985). Ultrasonic detectors may be used to identify bat presence at a roost, but are least preferable for exit-counts because detectors are unable to distinguish multiple detections of an individual from single detections of many individuals. The accuracy of counts using human observers will vary with observer experience, number of bats present, and amount of vegetative clutter surrounding the exit. The effectiveness of human observers may be increased by using night-vision equipment. Variance in results associated with using human observers may be estimated by using multiple observers at the same exit, or by using a combination of observers and electronic devices (e.g., beam-splitter count devices, video recorders, and photographic equipment). Digital infrared video recorders alone or coupled with ultrasonic detection devices represent a promising new method for obtaining exit counts at roosts with minimal observer bias, because recorded emergence activity can be replayed at reduced speed to facilitate accurate counts of exiting bats (Bob Berry, pers. comm.). In addition to improving the accuracy of counts, electronic devices may be used at inaccessible roosts and

may be easily deployed at multiple sites. However, electronic devices may not be feasible in areas of frequent human activity and they require reliable power sources, which may limit the utility of the devices.

Results from Sherwin et al (2000) indicate that colonies of *C. townsendii* that use caves exhibit higher sight fidelity, across both time and space, than colonies that use abandoned mines, suggesting that more than one visit will probably be required to establish non-use of a mine by bats. Sherwin et al. (2003) modeled lability in roost occupancy by big-eared bats throughout the Great Basin of the United States using data collected through internal surveys, exit surveys with low-light binoculars and infrared video cameras, and mist-nets set at the cave or mine entrance. They determined that, on average, four surveys were required to eliminate a mine as a maternity roost with 90% probability, whereas maternity colonies demonstrated high fidelity to cave sites, using a single cave for the duration of the maternity season and among years. A minimum of 9 surveys was required to eliminate a mine as a bachelor roost, while only 3 surveys, on average, were needed to eliminate a cave as a bachelor roost with 90% probability. Potential hibernacula required at least 8 surveys to be 90% sure that they were not used, although greater fidelity was shown by large colonies (≥ 5 individuals) than by small colonies (< 5 individuals), with large colonies requiring a minimum of 2 surveys and small colonies requiring at least 10 surveys.

Evaluation of Habitat Use

Studies designed to evaluate use of habitat by bats most often involve the use of lightweight radio-transmitters, light-tags, and acoustic detectors (Barclay and Bell 1988). One advantage of acoustic surveys over light-tags and radio-transmitters is that data collection can occur across seasons (i.e., through different reproductive stages) and is not dependent on capturing and handling bats. The limitations of acoustic detectors are noted above, and the importance of clearly articulating assumptions when evaluating trends in habitat use as assessed by detectors has been

addressed by Gannon et al. (2003). In some instances, small chemiluminescent tags (Buchler 1976) have been used to observe habitat use by bats (e.g., Aldridge and Rautenbach 1987), however, this method may be of limited use because of difficulties in observing the marked animals.

With the recent advent of small, lightweight radio-transmitters, the ability of researchers to monitor movements by bats has been greatly enhanced. In general, bats are captured, radio-transmitters are temporarily affixed to the dorsum of the bat, and the bats are released. A bat's foraging patterns can then be tracked via direct simultaneous triangulation (e.g., Lacki et al. 1994, Waldien and Hayes 2001), and its daily movements can be recorded by following the transmitter signal to a roost. Analysis usually proceeds by comparing characteristics of known roosts and foraging areas to that at randomly selected sites. Limitations of the use of radio-transmitters on bats include short battery life (2-3 weeks for most commercially available transmitters), which places greater importance on the understanding of seasonal and physiological effects on habitat use by bats when interpreting results, limited range of the transmitter (1-2 km in most situations) and the need to find individuals of sufficient mass to carry a transmitter without substantially altering its foraging ability and behavior (Aldridge and Brigham 1988).

Population and Habitat Management

The life histories of bats as a group suggest an evolutionary history of stable populations near or at the limit of the environment's carrying capacity (Findley 1993). If so, ecological theory would predict that an increase in population numbers might be realized from an increase in suitable habitat (Gotelli 2001). Indeed, current management plans for *C. townsendii* focus on increasing habitat (particularly roosting habitat) as a means of increasing numbers of bats (e.g., USFWS 1979; Pierson et al. 1999; Altenbach et al. 2002). Yet, despite the cavernicolous

tendencies of *C. townsendii*, many of the apparently abundant cave- and mine-roosting structures seem not to be used by bats, while some are used selectively and/or only at specific times of the year (Pearson et al. 1952, Graham 1966).

The ability to conserve energy stores is absolutely crucial to overwinter survival of hibernating bats. Therefore suitable hibernacula play a critical role in the year-to-year viability of the populations of bats using them. Historically, roosting habitat for *C. townsendii* presumably consisted of caves, lava tubes, or similar naturally occurring cavernous structures, but the bat now also uses abandoned mines and buildings. Yet, despite this apparent increase in roosting habitat, abundance of *C. townsendii* seems to be declining. So has the introduction of abandoned mines and buildings on the landscape been beneficial to big-eared bats? Altenbach and Sherwin (2002) proposed that the effects of the creation of abandoned mines on bats is equivocal due to a lack of baseline data on historical population densities and whether or not population sizes are limited by lack if roosts.

Efforts to manage populations should be most beneficial when habitat critical to *C. townsendii* is successfully protected from destruction and unwarranted disturbance. For instance, because *C. townsendii* is notably sensitive to human disturbance of roosts (e.g., Pearson et al. 1952; Graham 1966; Humphrey and Kunz 1976; Pierson and Rainey 1996), seasonal or permanent closures may be required for caves or mines that are deemed to be important as hibernacula or maternity roosts.

As noted above in Area Requirements, during the latter stages of reproduction (lactation and post-lactation), females of the two eastern subspecies (*C. t. ingens* and *C. t. virginianus*) appear to increase their foraging areas (Clark et al. 1993; Adam et al. 1994), apparently in order to meet the increased energetic demands of lactation or to allow newly volant young to exploit the nearby foraging areas. In either case, an increase in energy expenditure by females results, and it is

particularly pronounced during lactation when females must return to the roost during the night to nurse the young. An implicit but untested conclusion of this discussion is that if the foraging habitat were productive enough, females would not have to travel greater distances to meet energetic requirements. If so, then productive foraging habitat in close proximity to nursery roosts would be disproportionately beneficial, and should be afforded special management consideration. Given the tight energy budgets of nearctic insectivorous bats, the ability to forage efficiently is crucial, particularly for pregnant or lactating females whose energetic demands are increased. Therefore, multiple foraging areas within cost-efficient flight distance from roosts may be important components of the landscape for bats.

To the extent that climate change – human-mediated or otherwise – alters the distribution and density of their prey, bats will be forced to follow this shifting prey-base. Species that require specialized roosting habitat may be deleteriously impacted under this scenario if suitable habitat is less abundant in the new range (Bogan 1997, Humphries et al. 2002).

Results from a number of studies indicate that efforts designed to reduce disturbance at roost sites are both viable and fruitful. For example, numbers of *C. t. virginianus* and *Myotis sodalis* increased at 10 caves in West Virginia in the 12 years following protection of the sites (Stihler and Hall 1993). Mitigation efforts for *C. townsendii* in California proved successful despite proximity to active mines (Pierson et al. 1991). Although proper gate design and construction can enhance the quality of the cave or mine, improper designs can degrade the quality by altering internal airflow and temperature (Dalton and Dalton 1995).

Captive Propagation and Reintroduction

To our knowledge, no propagation programs exist or are planned for this species. Given the current population status of *C. townsendii*, existing conservation funds would be best spent on

identification and protection of suitable habitat, particularly that habitat associated with maternity colonies and hibernacula. If population declines become so pronounced that captive propagation and reintroduction becomes necessary, its success would be questionable without substantial further research. Although many species of bats have been kept in captivity for the purpose of research (Wilson 1988), Townsend's big-eared bat does not appear to do well in captivity (Pearson et al. 1952). Moreover, it is unclear if bats raised in a laboratory would be able to fend for themselves once released.

Information Needs

As noted above in *Habitat Trends*, the exact interplay of internal and external characteristics of preferred roosting sites are largely unknown. Faced with a mandate for conservation measures, frequently in the absence of precise knowledge, managers often fall back on a Kinsellian philosophy: "If you build it, they will come." In the manifestation of that philosophy germane here, some structures that harbor bats or that have the potential to harbor bats have been gated or seasonally closed. In all likelihood this approach has benefited Townsend's big-eared bats and other cavernicolous species of bats. However, efforts to conserve viable populations of bats solely through the preservation of roosting habitat may fall short; we must be also consider the quantity and quality of the surrounding foraging and drinking habitat. Moreover, "we don't clearly understand the constraints limiting population sizes [of big-eared bats] and whether or not these have been relieved through the creation of additional roosts." (Altenbach and Sherwin 2002).

Pierson et al. (1999) identified four research goals, the foci of which are to fill gaps in our understanding and to inform management decisions regarding *C. townsendii*. They are: 1) assess the degree of variability in roosts throughout the species' range; 2) evaluate roost microclimate and structural parameters for predictive screening and site evaluation; 3) develop a better

understanding of foraging ecology, including habitat preferences, responses to land management activities, and baseline data on temporal distribution and abundance of insect prey in occupied areas; 4) examine the direct and indirect impacts of environmental toxicants, particularly pesticides, on populations.

To this list could be added the development of baseline estimates of population density for *C. townsendii*. Although the logistical hurdles to such an endeavor are not trivial, advancements in technology, combined with modeling efforts derived from the information noted above, should make the goal somewhat more tenable.

Tables and Figures

Table 1. Current federal and state status and heritage program rankings of *Corynorhinus townsendii* in Wyoming and adjacent states. See Appendix for description of rank codes.

Species or Subspecies	USFWS ^a	Global Rank	Colorado	Idaho	Montana	Nebraska	South Dakota	Utah	Wyoming
Corynorhinus									S1B ^b /S2N ^b ,
townsendii		G4	S2 ^b , SS ^d	$S2^b$	$S2^b$	S1 ^b	S2S3 ^b	S3 ^b	NSS2 ^c , SS ^d
C. t. ingens	Е	G4T1					_		_
C. t. pallescens	C2	G4T4	S2 ^b	S2? ^b			_		_
C. t. townsendii	C2	G4T3T4		S2? ^b			_		
C. t. virginianus	Е	G4T2					_		_

Notes: A dash (—) indicates that the taxon likely does not occur in the state.

- a. C2 = Former USFWS Category 2 species of concern; E = Endangered
- b. Indicates Natural Heritage Rank
- c. Indicates Fish and Wildlife Program Rank
- d. Indicates State BLM Rank; SS = Sensitive Species

Fig. 1. The very large ears and fleshy lump on the nose (pararhinal gland) make *C. townsendii* distinguishable from other North American bats. Figure 1a. from Menzel et al. 2002. Figure 1b. by Phil Henry.

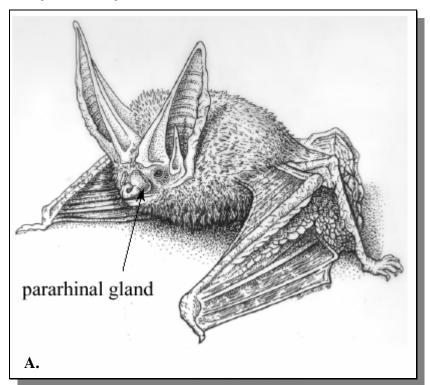




Fig. 2. Photograph of *C. townsendii* in flight. Photograph by J. Scott Altenbach, University of New Mexic, from Kunz and Martin (1982).



Fig. 3. Picture of *C. townsendii* at rest but alert. Photograph by M. Tuttle.



Fig. 4. Eastern big-eared bats (*C. rafinesquii*) showing ears coiled (A) and uncoiled (B). From Nowak 1994.

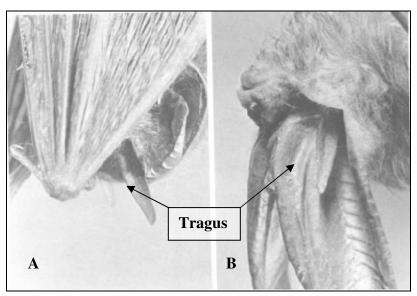


Fig. 5. Sonogram of the echolocation call of *C. townsendii* recorded by an Anabat® frequency-division detector. The *x*- and *y*-axes represent time (ms) and frequency (kHz) respectively. This call is about 150 ms long and the fundamental harmonic sweeps from 40 to 30 kHz. The upper set of pulses represents a secondary harmonic. Note that the frequency of the pulses that comprise the call change quickly relative to time. This type of downward-sweeping frequency modulated (FM) call is typical of many Vespertilionids, particularly those that forage in and around vegetative clutter or glean insects directly from vegetation.

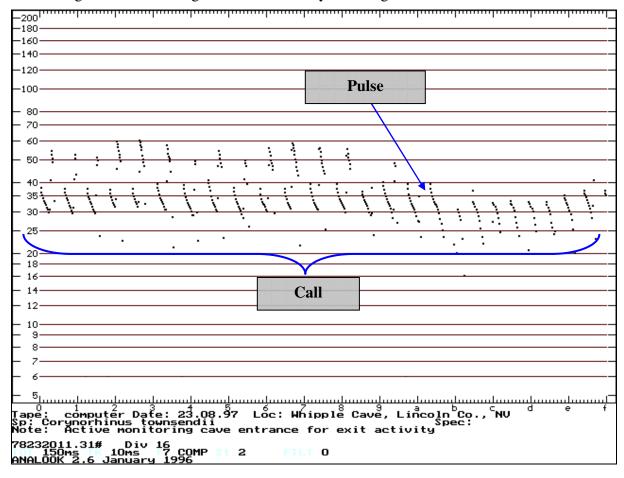


Fig. 6. Range-wide distribution of *C. townsendii*. The continuous range in the western portion of North America (A) represents *C. t. townsendii*, occurring along the west coast, and *C. t. pallescens*, occurring in the interior west. The disjunct ranges in the southern Midwest (B) and east-central (C) United States represent *C. t. ingens* and *C. t. virginianus* respectively.

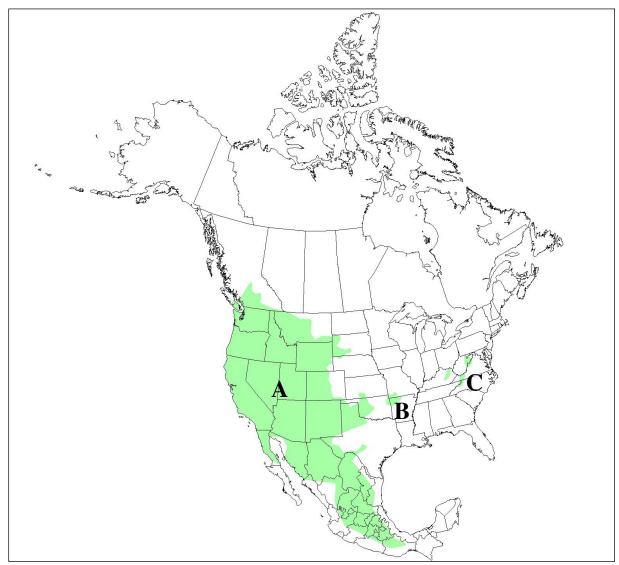


Fig. 7. Range and known occurrences for *C. townsendii* in Wyoming. Solid squares represent occurrences reported or verified since 1980, while gray triangles are records from prior to 1980. Data on occurrences are from the WYNDD database.

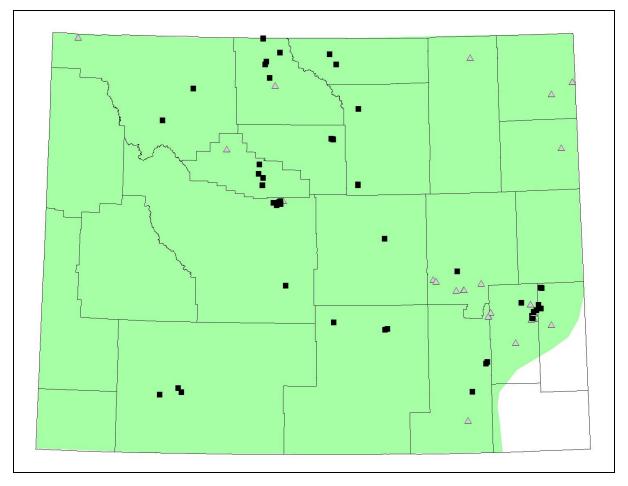
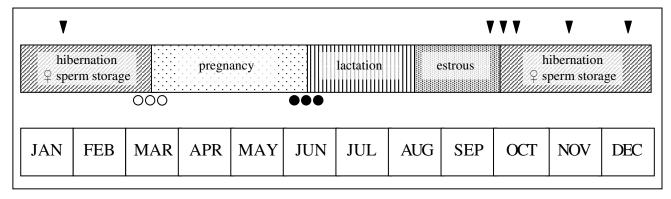


Fig. 8. Schematic of the timing of reproductive events for female C. townsendii. Inverted triangles designate probable copulatory periods. Open circles represent timing of ovulation. Closed circles represent parturition. Precise beginning and ending dates for these events vary with geographic location and environmental conditions. Adapted from Hill and Smith (1984).



Literature Cited

- Adam, M. D., and J. P. Hayes. 2000. Use of bridges as night roosts by bats in the Oregon Coast Range. Journal of Mammalogy 2:402-407.
- Adam, M. D., M. J. Lacki, and T. G. Barnes. 1994. Foraging areas and habitat use of the Virginia big-eared bat in Kentucky. Journal of Wildlife Management **58**:462-469.
- Adam, M. D., M. J. Lacki, and L. G. Shoemaker. 1994. Influence of environmental conditions on flight activity of *Plecotus townsendii virginianus* (Chiroptera: Vespertilionidae). Brimleyana **21**:77-85.
- Aldridge, H. D. J. N. 1986. Manoeuverability and ecological segregation in the little brown (*Myotis lucifugus*) and Yuma (*Myotis yumanensis*) bats (Chiroptera: Vespertilionidae). Canadian Journal of Zoology **64**:1878-1882.
- Aldridge, H. D. J. N., and R. M. Brigham. 1988. Load carrying and maneuverability in an insectivorous bat: a test of the 5% "rule" of radio-telemetry. Journal of Mammalogy **69**:379-382. Canadian Journal of Zoology **64**:1878-1882.
- Aldridge, H. D. J. N., and I. L. Rautenbach. 1987. Morphology, echolocation and resource partitioning in insectivorous bats. Journal of Animal Ecology **56**:763-778.
- Allen, G. M. 1916. Bats of the genus *Corynorhinus*. Bulletin of the Museum of Comparative Zoology **60**:332-358.
- Allen, H. 1865. On a new genus of Vespertilionidae. Proceedings of the Academy of Natural Sciences of Philadelphia **17**:173-175.
- Altenbach, J. S. 1998. Abandoned mines as bat habitat. Cultural Resource Management. **21**:46-48. Available: http://crm.cr.nps.gov/archive/21-7/21-7-18.pdf.
- Altenbach, J. S., W. Amy, P. V. Bradley, P. E. Brown, K. Dewberry, D. B. Hall, J. Jeffers, B. Lund, J. E. Newmark, M. J. O'Farrell, M. Rahn, R. E. Sherwin, C. R. Tomlinson, J. A. Williams. 2002. Nevada Bat Conservation Plan. Nevada Bat Working Group. Austin, Nevada. 188 pp.
- Altenbach, J. S., and R. E. Sherwin. 2002. Importance of protecting mines. *In* K. C. Vories and D. Throgmorton, editors. Proceedings of Bat Gate Design: A Technical Interactive Forum, Austin, Texas. U.S. Department of Interior, Office of Surface Mining, Alton, Illinois, USA. Available: http://www.mcrcc.osmre.gov/PDF/Forums/Bat%20Gate/1-2.pdf.
- Altenbach, J. S., and H. Milford. 1995. Evaluation and management of bats in abandoned mines in the Southwest. Pages 326-330 *in* D. Pate, editor. Proceedings of the 1993 National Cave Management Symposium, Carlsbad, New Mexico. American Cave Conservation Association, Horse Cave, Kentucky, USA.
- Andrewartha, H.G., and L.C. Birch. 1984. The ecological web: more on the distribution and abundance of animals. University of Chicago Press, Chicago, Illinois, USA.
- Anthony, E. L. P., M. H. Stack, and T. H. Kunz. 1991. Night roosting and the nocturnal time budget of the little brown bat, *Myotis lucifugus*: effects of reproductive status, prey density, and environmental conditions. Oecologia **51**:151-156.
- Arlettaz, R. 1999. Habitat selection as a major resource partitioning mechanism between the two sympatric sibling bat species *Myotis myotis* and *Myotis blythii*. Journal of Animal Ecology **68**:460-471.
- Bagley, F. M. 1984. A recovery plan for the Ozark big-eared bat and the Virginia big-eared bat. U.S. Fish and Wildlife Service, Twin Cities, Minnesota, USA.
- Bagley, F., and J. Jacobs. 1985. Census technique for endangered big-eared bats proving successful. Endangered Species Technical Bulletin **10**:5-7.

- Barbour, R. W., and W. H. Davis. 1969. Bats of America. University Press of Kentucky, Lexington, Kentucky, USA.
- Barclay, R. M. R. 1982. Night roosting behaviour of the little brown bat (*Myotis lucifugus*). Journal of Mammalogy **66**:782-783.
- Barclay, R. M. R. 1999. Bats are not birds a cautionary note on using echolocation calls to identify bats: a comment. Journal of Mammalogy **80**:290-296.
- Barclay, R. M. R., and G. P. Bell. 1988. Marking and observational techniques. Pages 59-76 *in* T. H. Kunz, editor. Ecological and Behavioral methods for the study of bats. Smithsonian Institution Press, Washington, D.C., USA.
- Barclay, R. M. R., and L. D. Harder. 2003. Life histories of bats: life in the slow lane. Pages 209-253 *in* T. H. Kunz and M. B. Fenton, editors. Bat ecology. University of Chicago Press, Chicago, Illinois, USA.
- Belwood, J. J., and R. J. Waugh. 1991. Bats and mines: abandoned does not always mean empty. BATS. 9:13-16.
- BLM Wyoming. 2001. Instruction memorandum no. WY-2001-040, sensitive species policy and list. Bureau of Land Management, Wyoming State Office, 5353 Yellowstone Road, PO Box 1828, Cheyenne, Wyoming. Available: www.wy.blm.gov/newsreleases/2001/apr/4_6_sensitivespecies.html.
- Bogan, M. A. 1997. Potential effects of global change on bats. Available: http://geochange.er.usgs.gov/sw/impacts/biology/bats/
- Bogdanowicz, W., S. Kaspar, and R. D. Owen. 1998. Phylogeny of plecotine bats: reevaluation of morphological and chromosomal data. Journal of Mammalogy **79**:78-90.
- Bradley, P. V. 1996. Foraging activity of adult female pale big-eared bats (*Corynorhinus townsendii pallescens*) in east-central Nevada (Abstract). Bat Research News **37**:21.
- Buchler, E. R. 1976. A chemiluminescent tag for tracking bats and other small mammals. Journal of Mammalogy **57**:173-176.
- Burford, L. S., and M. J. Lacki. 1998. Moths consumed by *Corynorhinus townsendii virginianus* in eastern Kentucky. American Midland Naturalist **139**:141-146.
- Caswell, H. 1989. Matrix population models: construction, analysis, and interpretation Sinauer Associates, Sunderland, Massachusetts, USA.
- Caswell, H. 2000. Matrix population models: construction, analysis, and interpretation. Second edition. Sinauer Associates, Sunderland, Massachusetts, USA.
- Clark, B. K., B. S. Clark, D. M. Leslie, Jr., and M. S. Gregory. 1996. Characteristics of caves used by the endangered Ozark big-eared bat. Wildlife Society Bulletin. 24:8-14.
- Clark, B. S. 1991. Activity patterns, habitat use, and prey selection by the Ozark big-eared bat (*Plecotus townsendii ingens*). PhD Dissertation, Oklahoma State University, Stillwater, Oklahoma, USA.
- Clark, B. S., D. M. Leslie, Jr., and T. S. Carter. 1993. Foraging activity of adult female Ozark big-eared bats (*Plecotus townsendii ingens*) in summer. Journal of Mammalogy **74**:422-427.
- Clark, D. R., Jr. 1981. Bats and environmental contaminants: a review. US Fish and Wildlife Service Special Scientific Report Wildlife Number 235. Washington, DC, USA.
- Clark, D. R., Jr. 1988a. Environmental contaminants and the management of bat populations in the United States. Pages 409-413 *in* R. C. Szaro, K. E. Severson, and D. R. Patton, editors. Management of amphibians, reptiles, and small mammals in North America. General Technical Report RM-166. USDA Forest Service, Rocky Mountain Forest and Range Experiment Station, Ft. Collins, Colorado, USA.

- Clark, D. R., Jr. 1988b. How sensitive are bats to insecticides? Wildlife Society Bulletin 16:399-403.
- Clark, D. R., Jr., and R. L. Hothem. 1991. Mammal mortality at Arizona, California, and Nevada gold mines using cyanide extraction. California Fish and Game 77:61-69.
- Clark, D. R., Jr., and A. Krynitsky. 1978. Organochlorine residues and reproduction in the little brown bat, Laurel, Maryland 1976. Pesticide Monitoring Journal **10**:44-53.
- Clark, D. R., Jr., and T.G. Lamont. 1976. Organochlorine residues and reproduction in the big brown bat. Journal of Wildlife Management **40**:249-254.
- Clark, D. R., Jr., and R. F. Shore. 2001. Chiroptera. Pages 159-214 *in* R. F. Shore and B. A. Rattner, editors. Ecotoxicology of wild mammals. John Wiley & Sons, West Sussex, UK.
- Clark, D. R., Jr., C. O. Martin, and D. M. Swineford. 1975. Organochlorine insecticide resifues in the free-tailed bat (*Tadarida brasiliensis*) at Bracken Cave, Texas. Journal of Mammalogy **56**:84-91.
- Clark, D. R., Jr., F. M. Bagley, and W. W. Johnson. 1988. Northern Alabama colonies of the endangered bat *Myotis grisescens*: organochlorine contamination and mortality. Biological Conservation **43**:38-45.
- Clark, T. W., and M. R. Stromberg. 1987. Mammals in Wyoming. University Press of Kansas, Lawrence, Kansas, USA.
- Cochran, M.E., and S. Ellner. 1992. Simple methods for calculating age-based life history parameters for stage-structured populations. Ecological Monographs **62**:345-364.
- Constantine, D. G. 1979. An updated list of rabies-infected bats in North America. Journal of Wildlife Diseases **15**:347-349.
- Cooper, W. 1937. On two species of *Plecotus* inhabiting the United States Territory. Annals of Lyceum of Natural History, New York. **4**:71-75.
- Crome, F. H. J., and G. C. Richards. 1988. Bats and gaps: microchiropteran community structure in a Queensland rain forest. Ecology **69**:1960-1969.
- Dalquest, W. W. 1947. Notes on the natural history on the bat *Corynorhinus rafinesquii* in California. Journal of Mammalogy **28**:17-30.
- Dalton, D. C., and V. M. Dalton. 1995. Mine closure methods including recommended gate design. Pages 130-135 *in* B. R. Riddle, editor. Inactive mines as bat habitat: guidelines for research, survey, monitoring and mine management in Nevada. Biological Resource Research Center, University of Nevada, Reno, Nevada, USA.
- Dobkin, D. S., R. D. Gettinger, and M. C. Gerdes. 1995. Springtime movements, roost use, and foraging activity of Townsend's big-eared bat (*Plecotus townsendii*) in central Oregon. Great Basin Naturalist **55**:315-321.
- Doggart, N., L. Joesph, J. Bayliss, and E. Fanning. 1999. Manga Forest Reserve: a biodiversity study. East Usambara Conservation Area Management Programme, Technical Paper 41. Ministry of Natural Resources and Tourism, Forestry and Beekeeping Division, Tanzania.
- Farney, J., and E. D. Fleharty. 1969. Aspect ratio, loading, wing span, and membrane areas of bats. Journal of Mammalogy **50**:362-367.
- Fellers, G. M. 2000. Predation on *Corynorhinus townsendii* by *Rattus rattus*. Southwestern Naturalist **45**:524-527.
- Fellers, G. M., and E. D. Pierson. 2002. Habitat use and foraging behavior of Townsend's big-eared bat (*Corynorhinus townsendii*) in coastal California. Journal of Mammalogy **83**:167-177.

- Fertig, W., and B. Heidel. 2002. Wyoming plant species of special concern. Wyoming Natural Diversity Database, Laramie, Wyoming, USA. Available: http://uwadmnweb.uwyo.edu/wyndd/PDF_files/Other/2002spconcernall.pdf
- Fenton, M. B. 1982. Echolocation, insect hearing, and feeding ecology of insectivorous bats. Pages 261-286 *in* T. H. Kunz, editor. Ecology of bats. Plenum Press, New York, NY, USA.
- Fenton, M. B., S. Bouchard, M. J. Vonhof, and J. Zigouris. 2001. Time-expansion and zero-crossing period meter systems present significantly different views of echolocation calls of bats. Journal of Mammalogy **82**:721-727.
- Fenton, M. B., I. L. Rautenbach, S. E. Smith, C. M. Swanepoel, J. Grosell, and J. van Jaarsveld. 1994. Raptors and bats: threats and opportunities. Animal Behavior **48**:9-18.
- Fenton, M. B., C. G. van Zyll de Jong, G. P. Bell, D. B. Campbell, and M. Laplante. 1980. Distribution, parturition dates, and feeding of bats in south-central British Columbia. The Canadian Field-Naturalist **94**:416-420.
- Findley, J. S. 1993. Bats: a community perspective. Cambridge University Press, New York, NY, USA.
- Frost, D. R., and R. M. Timm. 1992. Phylogeny of plecotine bats (Chiroptera: "Vespertilionidae"): summary of the evidence and proposal of a logically consistent taxonomy. American Museum Novitates 3034:1-6.
- Galen, C. and C. Bohn. 1979. Gopher snake preys on western big-eared bat. The Murrelet **Spring**: 27-28.
- Gannon, W. L., and W. Bogdanowicz. 2000. Contributions to the study of bats: field use of acoustic detectors. Acta Chiropterologica 2:i-ii.
- Gannon, W. L., R. E. Sherwin, and S. Haymond. 2003. On the importance of articulating assumptions when conducting acoustic studies of habitat use by bats. Wildlife Society Bulletin. **31**:45-61.
- Geluso, K. 1978. Urine concentrating ability and renal structure of insectivorous bats. Journal of Mammalogy **59**: 312-323.
- Genter, D. L. 1986. Wintering bats of the upper Snake River plain: occurrence in lava-tube caves. Great Basin Naturalist **46**: 241-244
- Gotelli, N. J. 2001. A Primer of Ecology. 3rd edition. Sinauer Associates, Inc., Sunderland, MA USA.
- Gould, E. 1970. Echolocation and communication in bats. Pages 144-161 *in* B. H. Slaughter and D. W. Walton, editors. About bats: a chiropteran biology symposium. Southern Methodist Press, Dallas, Texas, USA.
- Graham, R. E. 1966. Observations on the roosting habits of the big-eared bat, *Plecotus townsendii*, in California limestone caves. Cave Notes **8**: 17-24.
- Grindal, S. D., T. S. Collard, R. M. Brigham, and R. M. R. Barclay. 1992. The influence of precipitation on reproduction by *Myotis* bats in British Columbia. American Midland Naturalist **128**:339-344.
- Haas, G. E., A. J. Beck, and P. Q. Tomich. 1983. Bat fleas (Siphonaptera: Ischnopsyllidae) of California. Bulletin of the Southern California Academy of Sciences **82**:103-114.
- Handley, C. O., Jr. 1959. A revision of American bats of the genera *Euderma* and *Plecotus*. Proceedings of the U.S. National Museum **110**:95-246.
- Hayes, J. P. 1997. Temporal variation in activity of bats and the design of echolocation-monitoring studies. Journal of Mammalogy **78**:514-524.
- Hayes, J. P., and J. C. Gruver. 2000. Vertical stratification of bat activity in an old-growth forest in western Washington. Northwest Science **74**:102-108.

- Hecker, K. R., and R. M. Brigham. 1999. Does moonlight change vertical stratification of activity by forest-dwelling insectivorous bats? Journal of Mammalogy **80**:1196-1201.
- Hill, J. E., and J. D. Smith. 1984. Bats: A Natural History. University of Texas Press, Austin, Texas, USA.
- Humphries, M. M., D. W. Thomas, and J. R. Speakman. 2002. Climate-mediated energy constraints on the distribution of hibernating mammals. Nature **418**: 313-316.
- Humphrey, S. R., and J. B. Cope. 1976. Population ecology of the little brown bat, *Myotis lucifugus*, in Indiana and north-central Kentucky. Special Publication no. 4. American Society of Mammalogists, Stillwater, Oklahoma, USA.
- Humphrey, S. R., and T. H. Kunz. 1976. Ecology of a Pleistocene relict, the western big-eared bat (*Plecotus townsendii*) in the southern Great Plains. Journal of Mammalogy **57**:470-494.
- Husar, S. L. 1976. Behavioral character displacement: evidence of food partitioning in insectivorous bats. Journal of Mammalogy **57**:331-338.
- Hutson, A. M., S. P. Mickleburgh, and P. A. Racey, (comp.). 2001. Microchiropteran bats: global status survey and conservation action plan. IUCN/SSC Chiroptera Specialist Group. IUCN, Gland, Switzerland and Cambridge, UK. Available: http://www.lubee.org/CSG.
- Jones, C. 1965. Ecological distribution and activity periods of bats of the Mogollon mountains area of New Mexico and adjacent Arizona. Tulane Studies in Ecology **12**:93-100.
- Kalcounis, M. C., K. A. Hobson, R. M. Brigham, and K. R. Hecker. 1999. Bat activity in the boreal forest: importance of stand type and vertical strata. Journal of Mammalogy. 80(2):673-682.
- Karlsson, B.-L., J. Eklöf, and J. Rydell. 2002. No lunar phobia in swarming insectivorous bats (family Vespertilionidae). Journal of Zoology **256**:473-477.
- Keeley, B. 1998. Bat use of bridges. Prepared for: Bureau of Land Management, Coos Bay District, North Bend, Oregon, USA. Prepared by: Brian Keeley. Bat Conservation International, Austin, Texas, USA.
- Kingston, T., G. Jones, A. Zubaid, and T. H. Kunz. 2000. Resource partitioning in rhinolophoid bats revisited. Oecologia **124**:332–342.
- Knox, J. J. 1983. Mammals of the northern Great Plains. University of Nebraska Press, Lincoln, Nebraska, USA.
- Krzanowski, A. 1973. Numerical comparison of Vespertilionidae and Rhinolophidae (Chiroptera: Mammalia) in the owl pellets. Acta Zooligica Cracoviensia **18**:133-140.
- Kunz, T. H. 1973. Resource utilization: temporal and spatial components of bat activity in central Iowa. Journal of Mammalogy **54**:14-32.
- Kunz, T. H. 1974. Reproduction, growth, and mortality of the vespertilionid bat, *Eptesicus fuscus*, in Kansas. Journal of Mammalogy **55**:1-13.
- Kunz, T. H. 1982. Lasionycteris noctivagans. Mammalian Species:1-5.
- Kunz, T. H. and A. Kurta. 1988. Capture methods and holding devices. Pp 1-30 *In* Ecological and behavioral methods for the study of bats. T. H. Kunz, editor. Smithsonian Institution Press, Washington D. C., USA.
- Kunz, T. H., and R. A. Martin. 1982. Plecotus townsendii. Mammalian Species 175:1-6.
- Lacki, M. J., M. D. Adam, and L. G. Shoemaker. 1994. Observations on seasonal cycle, population patterns and roost selection in summer colonies of *Plecotus townsendii virginianus* in Kentucky. American Midland Naturalist **131**:34-42.
- Lewis, S. E. 1995. Roost fidelity of bats: a review. Journal of Mammalogy 76:481-496.

- Limpens, H. J. G. A., and K. Kapteyn. 1991. Bats, their behaviour and linear landscape elements. Myotis **29**:39-47.
- Love, R. A., C. Webon, D. E. Glue, and S. Harris. 2000. Changes in the food of British barn owls (*Tyto alba*) between 1974 and 1997. Mammal Review **30**:107-129.
- McCracken, G. F., Y.-F. Lee, J. K. Westbrook, B. B. Balsley, and M. L. Jensen. 1997. High altitude foraging by Mexican free-tailed bats: vertical profiling using kites and hot air balloons. Bat Research News 38:117.
- McDonald, D. B., and H. Caswell. 1993. Matrix methods for avian demography. Pages 139-185 *in* D. Power, editor. Current ornithology, Volume 10. Plenum Press, New York, New York, USA.
- Meier, L., and J. Garcia. 2001. Importance of mines for bat conservation. Pages 17-28, *in* K. Vories and D. Throgmorton, editors. Bat conservation and mining, a technical interactive forum. Office of Surface Mining, USDI, Alton, IL and Coal Research Center, SIU, Carbondale, Illinois, USA. Available: http://www.mcrcc.osmre.gov/PDF/Forums/Bats%20and%20Mining/1b.pdf
- Menzel, M. A., J. M. Menzel, S. B. Castelberry, J. Ozier, W. M. Ford, and J. W. Edwards. 2002. Illustrated key to skins and skulls of bats in the southeastern and mid-Atlantic states. Research Note NE-376. USDA Forest Service, Newtown Square, Pennsylvania, USA.
- Miller, J. C. 1992. Effects of a microbial insecticide, *Bacillus thurengiensis kurstaki*, on nontarget Lepidoptera in a spruce-budworm infested forest. Journal of Research on the Lepidoptera **29**:267-276
- Morrison, D. W. 1978. Lunar phobia in a neotropical fruit bat, *Artibeus jamaicensis* (Chiroptera: Phyllostomidae). Animal Behavior **26**:852-855.
- Navo, K. 1995. Guidelines for external surveys of mines for bat roosts. Pages 49-54 *In* Riddle, B. R. (editor). Inactive mines as bat habitat: guidelines for research, survey, monitoring and mine management in Nevada. Biological Resources Research Center, University of Nevada, Reno.
- Navo, K. W. 1994. Guidelines for the survey of caves and abandoned mines for bats in Colorado. Unpublished report. Colorado Division of Wildlife, Monte Vista, Colorado, USA.
- NatureServe Explorer. 2001. NatureServe: An online encyclopedia of life [web application]. Version 1.6. Arlington, Virginia, USA. Available: http://www.natureserve.org/explorer. (Accessed: December 17, 2002).
- Norberg, U. M., and J. V. M. Rayner. 1987. Ecological morphology and flight in bats (Mammalia: Chiroptera): wing adaptations, flight performance, foraging strategy and echolocation. Philosophical Transactions of the Royal Society of London B **316**:355-427.
- Nowak, R. M. 1994. Walker's bats of the world. Johns Hopkins University Press, Baltimore, Maryland, USA.
- Neuweiler, G. 2000. The Biology of bats. E. Covey, translator. Oxford University Press, New York, New York, USA.
- O'Farrell, M. J., and W. L. Gannon. 1999. A comparison of acoustic versus capture techniques for the inventory of bats. Journal of Mammalogy **80**:24-30.
- O'Farrell, M. J., C. Corben, W. L. Gannon, and B. W. Miller. 1999. Confronting the dogma: a reply. Journal of Mammalogy **80**:297-302.
- O'Shea, T. J., and M. A. Bogan. 2000. Interim Report of the Workshop on Monitoring Trends in U.S. Bat Populations: Problems and Prospects. [On-line Interim Report]. U.S. Geological Survey, Midcontinent Ecological Science Center, Fort Collins, Colorado, 124 pp. Available: http://www.mesc.usgs.gov/products/data/bpd/ireport.asp.

- O'Shea, T. J. and T. A. Vaughan. 1999. Population changes in bats from Central Arizona: 1971-1997. Southwestern Naturalist 44:495-500.
- Oakleaf, B., A. Cerovski, and M. Grenier. 2002. Native species status matrix, March 2002. Appendix IV *in* A. O. Cerovski, editor. Threatened, endangered, and nongame bird and mammal investigations. Wyoming Game and Fish Department, Cheyenne, Wyoming, USA.
- Paige, K. N. 1995. Bats and barometric pressure: conserving limited energy and tracking insects from the roost. Functional Ecology **9**:463-467.
- Paradiso, J. L. and A. M. Greenhall. 1967. Longevity records for American bats. American Midland Naturalist **78**:251-252.
- Pearson, O. P., M. P. Koford, and A. K. Pearson. 1952. Reproduction of the lump-nosed bat (*Corynorhinus rafinesquei*) in California. Journal of Mammalogy **33**:273-320.
- Perkins J. M. 1994. Longevity records for two Vespertilionids. Bat Research News 35:79-80
- Perkins J. M., and C. Levesque. 1987. Distribution, status, and habitat affinities of Townsend's big-eared bat (*Plecotus townsendii*) in Oregon. Oregon Department of Fish and Wildlife Nongame Wildlife Program. Technical Report num. 86-5-01.
- Perlmeter, S. I. 1995. Bats and bridges: a field study of the thermal conditions and social organization of night roosts in the Willamette National Forest. MS. York University, North York, Ontario, Canada.
- Pfister, C.A. 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. Proceedings of the National Academy of Sciences, USA **95**:213-218.
- Pierson, E. D. and W. E. Rainey. 1996. The distribution, status, and management of Townsend's big-eared bat (*Corynorhinus townsendii*) in California. California Department of Fish and Game, Bird and Mammal Conservation Program Report 96-7, Sacramento, California. Available: www.dfg.ca.gov/hcpb/info/bm_research/ bm_pdfrpts/96_07.pdf.
- Pierson, E. D., W. E. Rainey, and D. M. Koontz. 1991. Bats and mines: experimental mitigation for Townsend's big-eared bat at the McLaughlin Mine in California. Proceedings of the Thorne Ecological Institute: Issues and technology in the management of impacted wildlife. 5:31-42
- Pierson, E. D., M. C. Wackenhut, J. S. Altenbach, P. Bradley, P. Call, D. Genter, C. E. Harris, B. L. Keller, B. Lengus, L. Lewis, B. Luce, K. W. Navo, J. M. Perkins, S. Smith, and L. Welch. 1999. Species conservation assessment and strategy for Townsend's big-eared bat (*Corynorhinus townsendii townsendii and Corynorhinus townsendii pallescens*). Idaho Department of Fish and Game, Boise, Idaho, USA.
- Prather, J. W., and J. T. Briggler. 2002. Use of caves by Ozark big-eared bats (*Corynorhinus townsendii ingens*) in Arkansas. American Midland Naturalist. **148**:193-197.
- Quay, W. B. 1970. Integument and derivatives. Pages 1-56 in W. A. Wimsatt, editor. Biology of bats: Volume 2. Academic Press, New York, New York, USA.
- Racey, P. A. 1979. The prolonged storage and survival of spermatozoa in Chiroptera. Journal of Reproduction and Fertility **56**:391-402.
- Racey, P. A. 1988. Reproductive assessment in bats. Pages 31-46 *in* T. H. Kunz, editor. Ecological and behavioral methods for the study of bats. Smithsonian Institution Press, Washington, DC, USA.
- Racey, P. A. and A. C. Entwistle. 2000. Life-history and reproductive strategies of bats. Pages 363-414 *in* E. C. Crichton and P. H. Krutzsch, editors. Reproductive biology of bats. Academic Press, San Diego, California, USA.

- Racey, P. A., and S. M. Swift. 1985. Feeding ecology of *Pipistrellus pipistrellus* (Chiroptera: Vespertilionidae) during pregnancy and lactation. I. Foraging behaviour. Journal of Animal Ecology **54**:205-215.
- Reidinger, R. F., Jr. 1972. Factors influencing Arizona bat population levels. PhD Disseration, University of Arizona, Tuscon, Arizona, USA.
- Reith, C. C. 1980. Shifts in time of activity by *Lasionycteris noctivagans*. Journal of Mammalogy **61**:104-108.
- Reith, C. C. 1982. Insectivorous bats fly in shadow to avoid moonlight. Journal of Mammalogy **63**: 685-688.
- Sherwin, R. E., W. L. Gannon, J. S. Altenbach, and D. Stricklan. 2000. Roost fidelity of Townsend's bigeared bat in Utah and Nevada. Transactions of the Western Section of The Wildlife Society **36**:15-20.
- Sherwin, R. E., D. Stricklan, and D. S. Rogers. 2000. Roosting affinities of Townsend's big-eared bat (*Corynorhinus townsendii*) in northern Utah. Journal of Mammalogy **81**:939-947.
- Sherwin, R. E., W. L. Gannon, and J. S. Altenbach. 2003. Managing complex systems simply: understanding the inherent variation in the use of roosts by Townsend's big-eared bat. Wildlife Society Bulletin **31**:62-72.
- Speakman, J. R. 1995. Chiropteran nocturnality. Pages 187-201 *in* P. A. Racey and S. M. Swift, editors. Ecology, evolution and behaviour of bats. Oxford University Press, New York, New York, USA.
- Speakman, J. R., P. I. Webb, and P. A. Racey. 1991. Effects of disturbance on the energy expenditure of hibernating bats. Journal of Applied Ecology **28**:1087-1104.
- Stihler, C. W., and J. S. Hall. 1993. Endangered bat populations in West Virginia caves gated or fenced to reduce human disturbance. Bat Research News **34**:130.
- Theis, M. L., and K. McBee. 1994. Cross-placental transfer of organochlorine pesticides in Mexican free-tailed bats from Oklahoma and New Mexico. Archives of Environmental Contamination and Toxicology 27:239-242.
- Thomas, D. W. 1995. Hibernating bats are sensitive to nontactile human disturbance. Journal of Mammalogy **76**:940-946.
- Thomas, D. W., M. Dorais, and J. M. Bergeron. 1990. Winter energy budgets and cost of arousals for hibernating little brown bats, *Myotis lucifugus*. Journal of Mammalogy. **71**:475-479.
- Thomas, D. W., and R. K. LaVal. 1988. Survey and census methods. Pp 77-90 *In* Ecological and behavioral methods for the study of bats. T. H. Kunz, editor. Smithsonian Institution Press, Washington D. C., USA.
- Tumlison, R., and M. Douglas. 1992. Parsimony analysis and phylogeny of the plecotine bats (Chiroptera: Vespertilionidae). Journal of Mammalogy **73**:276-285.
- Tuttle, M. D. 1977. Gating as a means of protecting cave dwelling bats. Pages 77-82 *in* T. Aley and D. Rhodes, editors. National cave management symposium proceedings. Speleobooks, Albuquerque, New Mexico, USA.
- Tuttle, M. D. 1974. An improved trap for bats. Journal of Mammalogy 55:475-477.
- Usman, K., R. Habersetzer, R. Subbaraj, G. Gopalkrishnaswamy, and K. Paramandam, 1980. Behaviour of bats during a lunar eclipse. Behavioral Ecology and Sociobiology 7:79-80.
- US Fish and Wildlife Service. 1979. Endangered and threatened wildlife and plants; listing of Virginia and Ozark big-eared bats as endangered species, and critical habitat determination. Federal Register 44:69206-69208.

- USDA Forest Service. 1994. FSM 5670 R2 Supplement No. 2600-94-2; Region 2 Sensitive Species List. USDA Forest Service, Rocky Mountain Region, Denver, Colorado, USA.
- Verboom, B., and H. Huitema. 1997. The importance of linear landscape elements for the pipistrelle *Pipistrellus pipistrellus* and the serotine bat *Eptesicus serotinus*. Landscape Ecology **12**:117-125.
- Waldien, D. L., and J. P. Hayes. 2001. Activity areas of female long-eared myotis in coniferous forests in western Oregon. Northwest Science **75**:307-314.
- Wethington, T. A., D. M. Leslie, Jr., M. S. Gregory, and M. K. Wethington. 1996. Prehibernation habitat use and foraging activity by endangered Ozark big-eared bats (*Plecotus townsendii ingens*). American Midland Naturalist. **135**:218-230.
- Wethington, T. A., D. M. Leslie, Jr., M. S. Gregory, and M. K. Wethington. 1997. Vegetative structure and land use relative to cave selection by endangered Ozark big-eared bats (*Corynorhinus townsendii ingens*). Southeastern Naturalist **42**:177-181.
- Whitaker, J. O., C. Maser, and L. E. Keller. 1977. Food habits of bats of western Oregon. Northwest Science **51**:46-55.
- Williams, G. C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist **100**:687-690.
- Wilson, D. E. 1988. Maintaining captive bats. Pages 247-264 *in* T. H. Kunz, editor. Ecological and Behavioral Methods for the Study of Bats. Smithsonian Institution Press, Washington, D.C., USA.
- WYNDD Database. 2001. Unpublished distribution information for *Corynorhinus townsendii* in Wyoming from the Biological and Conservation Data System of the Wyoming Natural Diversity Database. University of Wyoming, Laramie, Wyoming, USA.

Additional References

- Findley, J. S. 1976. The structure of bat communities. American Naturalist 110: 129-139.
- Findley, J. S., and H. L. Black. 1983. Morphological and dietary structuring of a Zambian insectivorous bat community. Ecology **64**: 625-630.
- Racey, P. A., and A. C. Entwhistle. 2003. Conservation ecology. Pages 680-743 *in* T. H. Kunz and M. B. Fenton, editors. Bat Ecology. University of Chicago Press, Chicago, Illinois, USA.
- Willig, M. R., and M. P. Moulton. 1989. The role of stochastic and deterministic processes in structuring neotropical bat communities. Journal of Mammalogy **70**: 323-329.

Appendix: Explanation of Ranking codes and Management Status abbreviations.

TABLE A-1. Wyoming Game and Fish Department Status Rankings¹

Rank	Definition
NSS1	Includes species with on going significant loss of habitat and with populations that are greatly restricted or declining (extirpation appears possible).
NSS2	Species in which (1) habitat is restricted or vulnerable (but no recent or significant loss has occurred) and populations are greatly restricted or declining; or (2) species with ongoing significant loss of habitat and populations that are declining or restricted in numbers and distribution (but extirpation is not imminent).
NSS3	Species in which (1) habitat is not restricted, but populations are greatly restricted or declining (extirpation appears possible); or (2) habitat is restricted or vulnerable (but no recent or significant loss has occurred) and populations are declining or restricted in numbers or distribution (but extirpation is not imminent); or (3) significant habitat loss is ongoing but the species is widely distributed and population trends are thought to be stable.

TABLE A-2. Global Heritage Status Rank Definitions.² Table adapted from NatureServe *Explorer* (2001).

Rank	Definition
GX	Presumed Extinct (species)—Believed to be extinct throughout its range. Not located despite intensive searches of historical sites and other appropriate habitat, and virtually no likelihood that it will be rediscovered.
	Eliminated (ecological communities)—Eliminated throughout its range, with no restoration potential due to extinction of dominant or characteristic species.
GH	Possibly Extinct (species)—Known from only historical occurrences, but may nevertheless still be extant; further searching needed.
	Presumed Eliminated (Historic, ecological communities)—Presumed eliminated throughout its range, with no or virtually no likelihood that it will be rediscovered, but with the potential for restoration, for example, American Chestnut (Forest).
G1	Critically Imperiled —Critically imperiled globally because of extreme rarity or because of some factor(s) making it especially vulnerable to extinction. Typically 5 or fewer occurrences or very few remaining individuals (<1,000) or acres (<2,000) or linear miles (<10).

¹ The Wyoming Game and Fish Department has developed a matrix of habitat and population variables to determine the conservation priority of all native, breeding bird and mammal species in the state. Six classes of Native Status Species (NSS) are recognized, of which classes 1, 2, and 3 are considered to be high priorities for conservation attention.

² Where no distinction is made, definition is identical for species and ecological communities

TABLE A-2. Continued

RANK	DEFINITION			
G2	Imperiled —Imperiled globally because of rarity or because of some factor(s) making it very vulnerable to extinction or elimination. Typically 6 to 20 occurrences or few remaining individuals (1,000 to 3,000) or acres (2,000 to 10,000) or linear miles (10 to 50).			
G3	Vulnerable —Vulnerable globally either because very rare and local throughout its range, found only in a restricted range (even if abundant at some locations), or because of other factors making it vulnerable to extinction or elimination. Typically 21 to 100 occurrences or between 3,000 and 10,000 individuals.			
G4	Apparently Secure —Uncommon but not rare (although it may be rare in parts of its range, particularly on the periphery), and usually widespread. Apparently not vulnerable in most of its range, but possibly cause for long-term concern. Typically more than 100 occurrences and more than 10,000 individuals.			
G5	Secure —Common, widespread, and abundant (although it may be rare in parts of its range, particularly on the periphery). Not vulnerable in most of its range. Typically with considerably more than 100 occurrences and more than 10,000 individuals.			
Variant (Global Ranks			
G#G#	Range Rank —A numeric range rank (e.g., G2G3) is used to indicate uncertainty about the exact status of a taxon. Ranges cannot skip more than one rank (e.g., GU should be used rather than G1G4).			
GU	Unrankable —Currently unrankable due to lack of information or due to substantially conflicting information about status or trends. NOTE: Whenever possible, the most likely rank is assigned and the question mark qualifier is added (e.g., G2?) to express uncertainty, or a range rank (e.g., G2G3) is used to delineate the limits (range) of uncertainty.			
G?	Unranked—Global rank not yet assessed.			
НҮВ	Hybrid —(species elements only) Element not ranked because it represents an interspecific hybrid and not a species. (Note, however, that hybrid-derived species are ranked as species, not as hybrids.)			
Rank Qua	alifiers			
?	Inexact Numeric Rank—Denotes inexact numeric rank			
Q	Questionable taxonomy that may reduce conservation priority— Distinctiveness of this entity as a taxon at the current level is questionable; resolution of this uncertainty may result in change from a species to a subspecies or hybrid, or inclusion of this taxon in another taxon, with the resulting taxon having a lower-priority (numerically higher) conservation status rank.			
C	Captive or Cultivated Only—Taxon at present is extant only in captivity or cultivation, or as a reintroduced population not yet established.			
Infraspec	ific Taxon Ranks			
Т#	Infraspecific Taxon (trinomial) —The status of infraspecific taxa (subspecies or varieties) are indicated by a "T-rank" following the species' global rank. Rules for assigning T-ranks follow the same principles outlined above. For example, the global rank of a critically imperiled subspecies of an otherwise widespread and common species would be G5T1. A vertebrate animal population (e.g., listed under the U.S. Endangered Species Act or assigned candidate status) may be tracked as an infraspecific taxon and given a T rank; in such cases a Q is used after the T-rank to denote the taxon's informal taxonomic status.			

TABLE A-3. National (N) and Subnational (S) Heritage Status Rank Definitions.

RANK	DEFINITION
NX SX	Presumed Extirpated —Element is believed to be extirpated from the nation or subnation. Not located despite intensive searches of historical sites and other appropriate habitat, and virtually no likelihood that it will be rediscovered.
NH SH	Possibly Extirpated (Historical)—Element occurred historically in the nation or subnation, and there is some expectation that it may be rediscovered. Its presence may not have been verified in the past 20 years.
N1 S1	Critically Imperiled —Critically imperiled in the nation or subnation because of extreme rarity or because of some factor(s) making it especially vulnerable to extirpation from the subnation. Typically 5 or fewer occurrences or very few remaining individuals (<1,000).
N2 S2	Imperiled —Imperiled in the nation or subnation because of rarity or because of some factor(s) making it very vulnerable to extirpation from the nation or subnation. Typically 6 to 20 occurrences or few remaining individuals (1,000 to 3,000).
N3 S3	Vulnerable —Vulnerable in the nation or subnation* either because rare and uncommon, or found only in a restricted range (even if abundant at some locations), or because of other factors making it vulnerable to extirpation. Typically 21 to 100 occurrences or between 3,000 and 10,000 individuals.
N4 S4	Apparently Secure—Uncommon but not rare, and usually widespread in the nation or subnation*. Possible cause of long-term concern. Usually more than 100 occurrences and more than 10,000 individuals.
N5 S5	Secure —Common, widespread, and abundant in the nation or subnation*. Essentially ineradicable under present conditions. Typically with considerably more than 100 occurrences and more than 10,000 individuals.
N? S?	Unranked—Nation or subnation* rank not yet assessed.
NU SU	Unrankable—Currently unrankable due to lack of information or due to substantially conflicting information about status or trends.
N#N# S#S#	Range Rank—A numeric range rank (e.g., S2S3) is used to indicate the range of uncertainty about the exact status of the element. Ranges cannot skip more than one rank (e.g., SU is used rather than S1S4).
НҮВ	Hybrid —Element not ranked because it represents an interspecific hybrid, not a species.
NE SE	Exotic —An exotic established in the nation or subnation*; may be native in nearby regions (e.g., house finch or catalpa in eastern U.S.).
NE# SE#	Exotic Numeric —An exotic established in the nation or subnation* that has been assigned a numeric rank to indicate its status, as defined for N1 or S1 through N5 or S5.

¹ Subnational indicates jurisdictions at the state or provincial level (e.g. California, Ontario).

Table A-3. Continued

RANK	DEFINITION				
NA SA	Accidental—Accidental or casual in the nation or subnation,* in other words, infrequent and outside usual range. Includes species (usually birds or butterflies) recorded once or only a few times at a location. A few of these species may have bred on the one or two occasions they were recorded. Examples include European strays or western birds on the East Coast and vice-versa.				
NZ SZ	Zero Occurrences —Present but lacking practical conservation concern in the nation or subnation* because there are no definable occurrences, although the taxon is native and appears regularly in the nation or subnation*. An NZ or SZ rank will generally be used for long distance migrants whose occurrences during their migrations have little or no conservation value for the migrant, as they are typically too irregular (in terms of repeated visitation to the same locations), transitory, and dispersed to be reliably identified, mapped, and protected.				
NP SP	Potential—Potential that element occurs in the nation or subnation* but no extant or historic occurrences are accepted.				
NR SR	Reported —Element reported in the nation or subnation* but without a basis for either accepting or rejecting the report, or the report not yet reviewed locally. Some of these are very recent discoveries for which the program hasn't yet received first-hand information; others are old, obscure reports.				
NSYN SSYN	Synonym—Element reported as occurring in the nation or subnation*, but the national or state data center does not recognize the taxon; therefore the element is not assigned a national or subnational rank				
*	N or S rank has been assigned and is under review. Contact the individual subnational* Natural Heritage program for assigned rank.				
Not Provided	Species is known to occur in this nation or subnation.* Contact the individual subnational* Natural Heritage program for assigned rank.				
Breeding S	tatus Qualifiers				
В	Breeding—Basic rank refers to the breeding population of the element in the nation or subnation.*				
N	Nonbreeding—Basic rank refers to the non-breeding population of the element in the nation or subnation.*				
Other Qua	lifiers				
?	Inexact or Uncertain—Denotes inexact or uncertain numeric rank. For SE denotes uncertainty of exotic status. (The ? qualifies the character immediately preceding it in the SRANK.)				
C	Captive or Cultivated—Native element presently extant in the nation or subnation* only in captivity or cultivation, or as a reintroduced population not yet established.				