Townsend’s Big-eared Bat 
(*Corynorhinus townsendii*): 
A Technical Conservation Assessment

Prepared for the USDA Forest Service, 
Rocky Mountain Region, 
Species Conservation Project

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**COVER ILLUSTRATION CREDIT**

Townsend’s big-eared bat (*Corynorhinus townsendii*) in flight (© R. Smith). Original artwork by R. Smith. Used with permission.
SUMMARY OF KEY COMPONENTS FOR CONSERVATION OF TOWNSEND’S BIG-EARED BAT

There is general concurrence among bat biologists that there has been a downward trend in abundance of Townsend’s big-eared bat (*Corynorhinus townsendii*) in the western portion of its range over the past half-century. Western populations, which are the focus of this assessment, do not enjoy federal legislation protecting either them or their habitat. Various regional, state, and private organizations consider Townsend’s big-eared bat to be vulnerable to extirpation due to: 1) apparent rarity and long-term decline in numbers; 2) narrow roosting requirements; 3) loss, modification, and disturbance of roosting habitat; and 4) general lack of information regarding the species.

The likelihood of long-term persistence of Townsend’s big-eared bat in Region 2 and elsewhere can be enhanced by actions that address the primary threats to the species (listed below). Though we summarize the threats below in order of priority, it should be recognized that the best results will come from concurrently addressing these threats when crafting and implementing management plans.

- **Loss, modification, and disturbance of roosting habitat resulting from:**
  - **Uninformed closure of abandoned mines:** This is probably the most egregious act regularly performed by management agencies with respect to cavernicolous species of bats in general and Townsend’s big-eared bat specifically. At a minimum, closure of historic or abandoned mines eliminates potential roosting habitat for Townsend’s big-eared bat. In the worst case scenario, bats using a mine when it is closed have little chance of escape, resulting in both loss of habitat and direct loss of bats.
  - **Recreation:** Human activity at roosts, particularly recreational exploration of caves and mine interiors, may lead to abandonment of the roost or unnecessary expenditure of crucial energy reserves. Like other bats, Townsend’s big-eared bat is particularly sensitive to variations in survival and reproductive output. Therefore, human activity in and near roosts must be curbed, especially during reproductive and hibernal periods.
  - **Renewed mining at historical sites:** An increase in renewed mining can directly impact Townsend’s big-eared bats using abandoned mines in two ways:
    - by disturbing and displacing bats that may have been using a mine
    - by eliminating potential roosting habitat.
  
  Furthermore, renewed mining can liberate heavy metals and other toxic materials, leading to contaminated water impoundments. In either case, with its close association to abandoned mines and reliance on open water for drinking, Townsend’s big-eared bat may be more susceptible to ingestion of toxins following renewed mining at historical sites.

- **Loss, modification, and disturbance of foraging habitat resulting from:**
  - **Elimination of forest canopy:** Although Townsend’s big-eared bat forages in a variety of habitat types, its flight and echolocation style makes it well suited to forage among the canopies and along the edges of mature forested stands. This species typically does not use large clear-cuts or regenerating stands in early seral stages.
  - **Elimination or alteration of wetland habitat:** Forest wetlands represent abundant sources of insect prey and fresh water for drinking. Activities that reduce the productivity of wetlands likely impact local populations of Townsend’s big-eared bat by reducing the quality of important foraging and drinking sites. Activities that alter the surface and subsurface hydrology of wetlands, including draining, stream diversion, and removal of shrub and overstory vegetation (e.g., through logging or grazing), ultimately reduce the value of wetlands to this species. As well, activities that increase sediment loads into wetlands (e.g., logging, grazing, road construction, mining) likely alter wetland soil and water chemistry and thus have potential to decrease the value of the wetland to Townsend’s big-eared bats.
  - **Conversion of native shrub and grasslands to urban or agricultural uses:** Encroachment of urban development and agriculture into areas of native vegetation likely alters the composition and abundance of insect prey in an area, and may affect the ability of Townsend’s big-eared bat to find adequate prey. Encroachment may also disturb roosts by increasing the rate of human visitation, and increasing predation pressure from cats and other generalist predators associated with human settlement.
Exposure to environmental toxins: Pesticides and heavy metals, if ingested by bats, can cause death or reduce reproductive ability. Pesticide application can indirectly affect bats via reduction of insect prey. Accumulation of pesticides and their residues in fat and brain tissue of bats may represent under-appreciated sources of mortality and loss of reproductive output. In addition, when bats drink from water impoundments produced by industrial or mining activities, they risk ingesting toxins and heavy metals, which may result in mortality of the bats.

To insure the long-term persistence of Townsend’s big-eared bat in Region 2, the following conservation elements should be employed to address the noted threats, as discussed in the body of this assessment:

Institution of long-term education program: As with other species of bats, Townsend’s big-eared bat is often the victim of accidental or deliberate destruction, both to individual colonies and to their habitat. In part, this may result from commonly held misconceptions about bats and the lack of understanding by the public of the benefits that bats provide. Therefore, conveying the positive benefits of bats and dispelling baseless myths about them form the base for a strong management-oriented conservation program for this species.

Protection of known roosting sites: Townsend’s big-eared bats are extremely sensitive to disturbance at roosts sites, particularly during the reproductive season and during hibernation. Disturbances during these times likely contribute to reduced reproductive output. Populations are especially susceptible to variations in survival and reproductive output. Therefore, human activity in and near roosts must be minimized or eliminated, especially during reproductive and hibernal periods.

Assessment of patterns of roost use and movement: Townsend’s big-eared bat is often assumed to exhibit a high degree of roost-site fidelity. Although certain types of colonies may show high fidelity to roosts (e.g., maternity colonies in caves), others may not (e.g., hibernation colonies in mines). A better understanding of patterns of roost use and fidelity is necessary to adequately protect roosting habitat through time and to adequately assess population trends.

Timber harvest regimes, prescribed burns, and other vegetation management actions should strive to maintain a mosaic of mature forest canopy that can be perpetuated through time.

Elimination of exposure to toxins: Chronic exposure to pesticides and mining-related contaminants have probable but hard to quantify effects on Townsend’s big-eared bat and other species of bats. Efforts to remediate indirect sources of exposure to toxins and eliminate direct exposure will benefit this and other species of wildlife.

Monitoring of populations: To effectively assess the population status of and quantify the effectiveness of conservation practices on Townsend’s big-eared bat, systematic monitoring of known colonies must be initiated and conducted at local and regional scales.
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INTRODUCTION

This conservation assessment is one of many being produced for the Species Conservation Project for the Rocky Mountain Region (Region 2) of the USDA Forest Service (USFS). Townsend’s big-eared bat (Corynorhinus townsendii) is the focus of an assessment because it is a sensitive species within Region 2. Within the National Forest System, a sensitive species is a plant or animal whose population viability is identified as a concern by a Regional Forester because of significant current or predicted downward trends in abundance or in habitat capability that would reduce the species’ distribution [FSM 2670.5 (19)]. A sensitive species may require special management, so knowledge of its biology and ecology is crucial. This assessment addresses the biology, conservation status, and management of Townsend’s big-eared bat throughout its range, but with an emphasis on Region 2. This introduction defines the goal of the assessment, outlines its scope, and describes the process used in its production.

Goal of Assessment

Species conservation assessments produced as part of the Species Conservation Project are designed to provide land managers, biologists, and the public with a thorough discussion of the biology, ecology, conservation status, and management of certain species, based on available scientific knowledge. The assessment goals limit the scope of the work to critical summaries of scientific knowledge, discussion of broad implications of that knowledge, and outlines of information needs. The assessment does not seek to prescribe management. Rather, it provides the ecological background upon which management must be based and focuses on the consequences of changes in the environment that result from management (i.e., management implications). Furthermore, it cites management recommendations proposed elsewhere and examines management that has been implemented.

Scope and Limitations of Assessment

This assessment examines the biology, ecology, conservation status, and management of Townsend’s big-eared bat with specific reference to the geographic and ecological characteristics of USFS Region 2. Although much of the literature on the species synthesized herein may originate from field investigations outside the region, this document places that literature in the ecological and social contexts of the central Rocky Mountains.

Townsend’s big-eared bat comprises five recognized subspecies in the United States. Generally, three of the subspecies (Corynorhinus townsendii australis, C. townsendii pallescens, and C. townsendii townsendii) maintain a western distribution while the other two subspecies (C. townsendii ingens and C. townsendii virginianus) sustain isolated populations in the eastern portion of the continent. The focus of this assessment is on the western group, as neither member of the eastern group occurs in Region 2. Throughout this document, we may refer to these subspecies groupings as the western group and the eastern group, or generically as Townsend’s big-eared bats. Further, because of taxonomic uncertainty and morphological and ecological similarities within the western group, we refer simply to these bats as C. townsendii.

In producing the assessment, we reviewed refereed literature, non-refereed publications, research reports, and data accumulated by resource management agencies. Not all publications on Corynorhinus townsendii are referenced in the assessment, nor were all published materials considered equally reliable. The assessment emphasizes refereed literature because this is the accepted standard in science. Non-refereed publications and reports were incorporated when refereed information was otherwise unavailable. Additionally, assessing the efficacy of current management and conservation strategies for C. townsendii must remain speculative until data are available across broad spatial and temporal scales.

Treatment of Uncertainty

To foster an understanding of the conservation needs for Corynorhinus townsendii, this assessment develops a general depiction of the biology and requirements of the species, the information for which has been gleaned from a number of sources, some more reliable than others. Yet even the most reliable sources – those that withstood the scrutiny of peer evaluation – must not be considered infallible. Science progresses most surely when competing ideas about how the world works are measured against observations within an experimental framework that permits isolation of sources of variation (e.g., Hilborn and Mangel 1997). However, studies conducted on free-ranging animals, particularly those that are cryptic and capable of landscape-scale movements (e.g., bats) often are not tractable within an experimental framework. These types of studies, therefore, often rely on alternative approaches that, while useful, tend to limit the applicability of the results to the specific time and place in which the study occurred.
For species such as *Corynorhinus townsendii* that are generally rare and very patchy in distribution, these difficulties are magnified, and most research on the species has been qualitative and descriptive in nature. In this assessment, the strength of evidence for particular ideas is noted, and when appropriate, alternative explanations are described. While well-executed experiments represent a strong approach to developing knowledge, alternative approaches such as modeling, critical assessment of observations, and inference are accepted as sound approaches to understanding features of biology.

**Publication of Assessment on the World Wide Web**

To facilitate their use, species conservation assessments are being published on the Region 2 World Wide Web site. Placing the documents on the Web makes them available to agency biologists and the public more rapidly than publishing them as reports. More important, it facilitates revision or updating of the assessments, which will be accomplished based on protocols established by Region 2.

**Peer Review**

In keeping with the standards of scientific publication, assessments developed for the Species Conservation Project have been externally peer reviewed prior to their release on the Web. This assessment was reviewed through a process administered by the Society for Conservation Biology, which chose two recognized experts (on this or related taxa) to provide critical input on the manuscript.

**Management Status and Natural History**

**Management Status**

Western populations of Townsend’s big-eared bat (*Corynorhinus townsendii* pallescens and *C. townsendii townsendii*) are not currently listed under Federal Endangered Species legislation. However, they were formerly Candidate 2 (C2) species under the Endangered Species Act (U.S. Fish and Wildlife Service 1994) and are now considered a Species of Concern (non-statutory ranking) by the U.S. Fish and Wildlife Service (USFWS; **Table 1**). The USFWS has listed two eastern subspecies (*C. townsendii ingens* and *C. townsendii virginianus*) as endangered since 1979 (U.S. Fish and Wildlife Service 1979).

**Bureau of Land Management**

The Bureau of Land Management in Colorado and Wyoming consider *Corynorhinus townsendii* a sensitive species, defined as: (1) a species under status review by the USFWS/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) a species that inhabits ecological refugia or other specialized or unique habitats. (Bureau of Land Management Colorado 2000, Bureau of Land Management Wyoming 2001).

**Table 1.** Current federal and state status and Natural Heritage Program rankings of Townsend’s big-eared bat (*Corynorhinus townsendii*) in USDA Forest Service Region 2. See **Appendix A** for description of Rank codes.

<table>
<thead>
<tr>
<th>Species or Subspecies</th>
<th>USFWS Rank</th>
<th>Colorado</th>
<th>Kansas</th>
<th>Nebraska</th>
<th>South Dakota</th>
<th>Wyoming</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>C. townsendii</em></td>
<td>G4 / N4, N2N3</td>
<td>S2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>S2&lt;sup&gt;b&lt;/sup&gt;</td>
<td>S1&lt;sup&gt;b&lt;/sup&gt;</td>
<td>S2S3&lt;sup&gt;b&lt;/sup&gt;</td>
<td>S1B&lt;sup&gt;b&lt;/sup&gt;, S2N&lt;sup&gt;b&lt;/sup&gt;, NSS2&lt;sup&gt;c&lt;/sup&gt;</td>
</tr>
<tr>
<td><em>C. t. ingens</em></td>
<td>Endangered</td>
<td>G4T1</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>C. t. virginianus</em></td>
<td>Endangered</td>
<td>G4T2</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>C. t. pallescens</em></td>
<td>SPOC&lt;sup&gt;a&lt;/sup&gt;</td>
<td>G4T4</td>
<td>S2&lt;sup&gt;e&lt;/sup&gt;, SC&lt;sup&gt;c&lt;/sup&gt;</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
<tr>
<td><em>C. t. townsendii</em></td>
<td>SPOC&lt;sup&gt;a&lt;/sup&gt;</td>
<td>G4T3T4</td>
<td>—</td>
<td>—</td>
<td>—</td>
<td>—</td>
</tr>
</tbody>
</table>

<sup>a</sup>SPOC = Species of Concern (former USFWS C2 species)

<sup>b</sup>Indicates Natural Heritage Program Rank

<sup>c</sup>Indicates Fish and Wildlife Program Rank. SC = Species of Concern (non-statutory category); NSS2 = (Native Species Status 2): Species in which: populations are declining, extirpation appears possible; habitat is restricted or vulnerable but no recent or on-going significant loss; species may be sensitive to human disturbance, OR: populations are declining or restricted in numbers and/or distribution, extirpation is not imminent; ongoing significant loss of habitat.” (Wyoming Game and Fish Department 2005).

<sup>d</sup>Refer to **Appendix A** for detailed descriptions of Management Status Abbreviations used in this section.
Region 2 of the USFS ranks *Corynorhinus townsendii* as a sensitive species. Within the USFS, 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).

### State Wildlife Agencies

The Wyoming Game and Fish Department manages *Corynorhinus townsendii* Native Species Status 2 (NSS2). This designation is given to species for which either: “populations are declining, extirpation appears possible; habitat is restricted or vulnerable but no recent or on-going significant loss; species may be sensitive to human disturbance, or populations are declining or restricted in numbers and/or distribution, extirpation is not imminent; ongoing significant loss of habitat.” (Wyoming Game and Fish Department 2005). Wyoming also includes Townsend’s big-eared bat as a Species of Greatest Conservation Need in their Comprehensive Wildlife Conservation Strategy (Wyoming Game and Fish Department 2005).

Colorado and South Dakota consider Townsend’s big-eared bat a Species of Concern. Although this designation carries no statutory authority, bats in both states are listed as nongame species and as such are protected from unlawful take or possession (Colorado Revised Statutes §33-2-104; South Dakota Codified Laws §34A-8-6). In addition, Kansas and Nebraska consider *Corynorhinus townsendii* to be a nongame Species in Need of Conservation (Kansas Administrative Regulation §115-15-2; Nebraska Administrative Code §163-4-010). This designation is functionally equivalent to other state’s Species of Concern category. Species in Need of Conservation are not considered threatened or endangered and thus do not receive legal protection. However, they are protected from take or possession without permit (Kansas Administrative Regulation §115-15-2; Nebraska Administrative Code §163-4-010).

### Natural Heritage Ranks

NatureServe, the association of Natural Heritage organizations, ranks species’ status across their global (G ranks) and National (N ranks) ranges. The two western subspecies are regarded as G4 taxon, indicating that they are “apparently secure, although the species may be quite rare in parts of its range, especially at the periphery” (Keinath et al. 2003). Nationally, Townsend’s big-eared bat is considered an N4 species in the United States and an N2N3 species in Canada (Figure 1).

In addition to Global and National Ranks, each state or province ranks a species’ status within its own geopolitical boundaries (referred to as S rank). Within USFS Region 2, state heritage ranks for *Corynorhinus townsendii* include S1 (“Critically Imperiled”) in Nebraska and Wyoming, S2 (“Imperiled”) in Colorado and Kansas, and S2S3 (“Imperiled/Vulnerable”) in South Dakota (Table 1; see Table A1c for detailed descriptions of S ranks).

### Western Bat Working Group

The Western Bat Working Group (WBWG) considers Townsend’s big-eared bat a High Risk species throughout its range. A High Risk species, according to WBWG, is one that “should be considered the highest priority for funding, planning, and conservation actions” because “based on available information on distribution, status, ecology, and known threats, these species are imperiled or are at high risk of imperilment” (WBWG web page; http://www.wbwg.org/spp_matrix.html).

### Existing Regulatory Mechanisms, Management Plans, and Conservation Strategies

#### Regulatory mechanisms

To our knowledge, there are currently no federal or state regulatory mechanisms in place in Region 2 or elsewhere to provide specific statutory protection to the western subspecies of *Corynorhinus townsendii* or its habitat. However, cave and mine roosting habitat may be protected through one of several existing laws or regulations. A particularly useful resource for cave management on federal lands is available from the Umpqua National Forest (2004). This handbook outlines federal laws and USFS regulations pertaining to conservation and management of caves on federal lands. Among the laws and regulations are the Federal Cave Resources Protection Act (FCRPA), the Organic Administration Act, the Antiquities Act of 1906, and the Archeological Resources Protection Act (ARPA).

Seasional or permanent restrictions issued under Subpart B Orders, which are issued under authority of Section 16 of the United States Code (U.S.C.), may
protect roosting habitat in mines. In addition, the ARPA may be a vehicle for the protection of mines, provided that the mine is at least 100 years old and has some archeological importance. We discuss each act and its potential uses in the Tools and practices section below.

Management plans

There are no specific strategies at the federal level for conservation of Townsend’s big-eared bats in the West. However, because of the similarity in biology and ecology between the eastern and western subspecies, and because the effectiveness of management plans for eastern subspecies may suggest how similar actions would fare in the West, we briefly discuss the objectives set out for recovery of the eastern subspecies, and whether they have been effective.

The USFWS has listed the two eastern subspecies of Corynorhinus townsendii as endangered since 1979 (U.S. Fish and Wildlife Service 1979). The principal tenets of the recovery plan for both the Ozark and Virginia big-eared bats (C. townsendii ingens and C. townsendii virginianus, respectively) are to:

- obtain and/or maintain management authority of caves within the range.
census and monitor all known maternity colonies and hibernacula

- identify additional maternity colonies and hibernacula

- protect roosts from disturbance and destruction, and protect essential foraging habitat and movement corridors (U.S. Fish and Wildlife Service 1995).

The second and third goals pertain directly to management and conservation of the species and specify how population trends are to be monitored. The last goal sets out the management actions – protection of vital habitat components – expected to help the populations rebound. By all accounts, protection of these habitat components has been successful in halting or reversing population declines in the two subspecies. In a 2001-2002 report to Congress, USFWS indicated that numbers of Virginia big-eared bats were increasing and that recovery goals were 50 to 75 percent met. The recovery status of Ozark big-eared bats was lower (0 to 25 percent), but populations were listed as stable (U.S. Fish and Wildlife Service 2002). Inasmuch as these management objectives have been successful in mitigating population declines in the East, we suggest that western populations of Townsend’s big-eared bats also stand to benefit from similar protections.

Conservation strategies

Current conservation strategies consist of state-specific plans that address bat conservation for all bats within a state, and one multi-state plan that is specific to Townsend’s big-eared bat. All of these plans are similar in that they outline the natural history of the species included in the plans, identify threats to their persistence, and discuss hurdles to effective conservation of the bats.

Idaho conservation effort assessment and strategy for Townsend’s big-eared bat

The Species Conservation Assessment and Conservation Strategy for the Townsend’s Big-Eared Bat (Pierson et al. 1999) is a comprehensive summary of the status and conservation needs for Townsend’s big-eared bats in the West. At the broadest level, the goal of the Idaho Conservation Effort (ICE) was to identify “proactive conservation strategies for species at risk of being listed...under the Endangered Species Act” (Pierson et al. 1999). When considering Townsend’s big-eared bat, the ICE recognized that a state-specific conservation effort may be insufficient to address range-wide declines of the species. The ICE, therefore, invited participation from resource managers and researchers from other western states during the development of its conservation strategy for Corynorhinus townsendii. Representatives from seven western states and two federal agencies participated, and from this core group the Western Bat Working Group was formed in 1994. The conservation document for Townsend’s big-eared bat that resulted remains an excellent source of information and management strategies for the species, no doubt due in part to the strength of its interagency input and breadth of its geographic coverage. Being a seminal work in this regard and as testimony to its potential, the ICE strategy for Townsend’s big-eared bat was adopted by the Western Association of Fish and Wildlife Agencies (WAFWA)\(^2\).

The ICE strategy identified several key conservation elements and provided management guidelines aimed at protecting these elements. Among these guidelines were standards for management of caves and mines (including renewed mining at historical mines), toxic material impoundments associated with mining, pesticide spraying, vegetative conversions, and timber harvest. We will borrow and incorporate many of these guidelines in the Management section below, thus we will not go into further detail here. The reader is directed to the ICE document (Pierson et al. 1999) for more detail, and to the website of the Western Bat Working Group (http://www.wbwg.org/) for updates on the strategy.

Western states with general bat conservation strategies

Several western states have begun to address the conservation needs of bats through the development of documents outlining conservation needs and strategies for bats endemic to each particular state. To date, Arizona, Colorado, Nevada, and South Dakota have completed conservation plans for bats. Although the formats of the documents vary somewhat from state to state, each provides an overview of the conservation status of the bats found within the state and identifies important conservation elements (e.g., roosting habitat, foraging habitat). In addition, each was drafted by a group of management and research biologists with

\(^2\)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.
interest in or experience with bat management and conservation. Generally, this included members of each state’s Bat Working Group, which are, in turn, part of the Western Bat Working Group.

Consistent among the state plans is the implication of disturbance and destruction of roosts in local and range-wide declines of Townsend’s big-eared bat. Consequently, the plans promote, as core conservation elements for Corynorhinus townsendii, protection of known roosts and identification and protection of additional roosts. Although these documents are state-specific, the conservation strategies put forth may generally be considered applicable throughout the western range of C. townsendii.

**Arizona:** The Arizona Bat Conservation Strategic Plan (Hinman and Snow 2004) is based on the outline provided by the North American Bat Conservation Partnership’s State Planning Guide (Tuttle 2004), and it includes sections on resources important to bats such as roosts, foraging habitat, water, and migration corridors. Within each of these, a list of species that use each type of resource (e.g., cave roosts) and the threats to the resource are delineated.

For Corynorhinus townsendii, the Arizona plan identifies several priority actions including:

- understanding movement patterns and roost switching in cave and mine roosts
- identification of roosting and foraging habitat requirements
- evaluation of the effectiveness of bat-friendly cave closures
- evaluation of the effectiveness of such closures in mine reclamation.

In addition, the Arizona plan outlines strategies for long-term monitoring of historic and current known roosts to establish population estimates and trends; monitoring the effects of management actions, human disturbance, and artificial assistance (e.g., man-made watering holes) on bat populations; public outreach and education about the benefits of bats; and better understanding of the effects of urbanization on bat populations.

**Colorado:** The Colorado Bat Conservation Plan (Ellison et al. 2003a) identified Corynorhinus townsendii as the species with the highest conservation priority in Colorado based on consideration of five major categories that directly impact bats or their habitat:

- mining
- cave and crevice management practices
- forest management practices
- rangeland management practices
- urban development.

Within each of these categories key issues, goals, objectives, and management and research needs are identified.

The inclusion of urban development as a potential major impact on bats speaks to the thoroughness of this document, and such threats, though sometimes overlooked, should be a consideration in areas where rapid urban development encroaches upon native habitat. The spread of urban development into previously undeveloped areas may not impact roosting habitat directly (i.e., caves and mines are likely to remain intact), but previously isolated roosting habitat may experience greater human visitation if urban development occurs near these structures. As well, conversion of native vegetative communities to neighborhoods and commercial and industrial zones may change diversity and abundance of insect prey and fragment or eliminate foraging/commuting corridors.

**Nevada:** The Nevada Bat Conservation Plan (Altenbach et al. 2002) takes a hierarchical approach, outlining strategies for conservation of specific habitat types (called “Bat Habitat Conservation Guilds”) that are based first on roosting preferences (e.g., tree-dwelling, cave-dwelling, crevice-dwelling) and second on the foraging/watering habitat of the bats comprising them. Within each of the conservation guilds, high priority and secondary priority species and appropriate conservation strategies are listed.

In the Nevada Bat Conservation Plan, Corynorhinus townsendii is identified as a high priority species in one roosting guild (Natural Cave, Mine Shaft and Mine Adit Roosting Habitat) and two foraging/watering guilds (Water Source Foraging and Drinking Habitat; Forest Woodland Foraging Habitat). With regard to roosting habitat, the Nevada plan identifies as its major management goal the reversal of population declines seen at caves and mines throughout the state. Explicit strategies that are suggested to meet this goal...
include identification and protection of current and historic roosts and minimization of disturbance at and near known roosts.

South Dakota: The South Dakota Bat Conservation Plan (South Dakota Bat Working Group 2004) is novel in the emphasis placed on public education and outreach to help minimize threats to bats. Many of the threats are surmised to originate in a general lack of knowledge about bats by the public, and are exacerbated by commonly propagated misinformation about bats. Educating the public about the benefits of healthy bat populations and dispelling commonly held myths about bats can only help managers convince a skeptical public that conserving bats is worthwhile. The South Dakota plan also emphasizes inter-agency cooperation and data sharing within the state to meet research needs and coordinate conservation activities. This level of cooperation is likely to be key for many states faced with tight funding for non-game species of wildlife.

State Wildlife Grants Program

In addition to bat-specific conservation strategies, all 50 states are currently completing a Comprehensive Wildlife Conservation Strategy, as required by the Consolidated Appropriations Act of 2005 (Public Law 108-447) for federal funding through the State Wildlife Grants Program. This program is intended to augment the ability of state wildlife management agencies to manage and conserve wildlife, especially non-game species, by providing federal funding for wildlife in need of conservation and their habitat. States are required to compile a list of Species in Greatest Need of Conservation, and the comprehensive strategy must identify the means by which states will monitor and manage these species and their habitat. All five states within USFS Region 2 (i.e., Colorado, Kansas, Nebraska, South Dakota, Wyoming) include Townsend’s big-eared bat on their list of Species in Greatest Need of Conservation.

Biology and Ecology

Description and systematics

Morphology

Townsend’s big-eared bat is a medium-sized bat with overtly large ears and characteristic bilateral horseshoe-shaped lumps on the muzzle (Figure 2). The lumps, actually enlarged pararhinal glands that produce sebaceous secretions, are apparently involved in mating (Pearson et al. 1952, Quay 1970) and give the bat one of its common names, the lump-nosed bat. 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 and brown or buff at the tips (Kunz and Martin 1982). Length of ear and tragus are 30 to 39 mm (1.2 to 1.5 inches) and 11 to 17 mm (0.4 to 0.7 inches) respectively (Kunz and Martin 1982). The ears are erect and point slightly forward in flight. However, during torpor and hibernation, one or both ears may be coiled tightly along the head (in the shape of a ram’s horn) leaving only the long pointed tragus visibly erect (Barbour and Davis 1969). Length of the forearm ranges from 39 to 48 mm (1.5 to 1.9 inches) (Clark and Stromberg 1987). Overall length is 90 to 112 mm (3.5 to 4.4 inches), and mass of adults ranges from 5 to 13 g (0.17 to 0.46 oz.).

Females tend to be slightly larger than males (Kunz and Martin 1982). However, size is an equivocal and unreliable character, and females may be distinguished from males only upon examination of genitalia or the presence of mammary glands and nipples (Racey 1988). The altricial young are born naked with eyes closed and ears flaccid. In one study, neonates averaged 2.4 g (0.08 oz.) with a forearm of 16.6 mm (0.65 inches) at birth, with no significant difference in morphological characters between males and females (Pearson et al. 1952).

Within Region 2, Townsend’s big-eared bat is unlikely to be confused in hand with other species of bats. However, two species with morphological traits similar to Corynorhinus townsendii occur in Region 2 (Table 2). The spotted bat (Euderma maculatum) occurs in western portions of Colorado and Wyoming and may be associated with caves and mines (Watkins 1977). It lacks pararhinal glands on the muzzle, and it has very large ears. The spotted bat can be distinguished from Townsend’s big-eared bat primarily by its larger, broader, and paler ears and by its distinctive pelage. Spotted bats also have black dorsal fur with contrasting white spots on the shoulders and rump, and white ventral fur.

Another morphologically similar species, the pallid bat (Antrozous pallidus), occurs in western Colorado, south-central Kansas, and the interior of Wyoming outside of the northwestern mountains, northeastern grasslands, and extreme southeastern corner of the state. Pallid bats have pararhinal glands on the muzzle, but they are not as pronounced as those in Townsend’s big-eared bats are. Pallid bats differ in appearance from Townsend’s big-eared bats primarily...
Figure 2. Distinguishing features of Townsend’s big-eared bat. The very large ears and fleshy lump on the nose (pararhinal gland) differentiate this species from other North American bats. A) adapted from Menzel et al. 2002. B) by Phil Henry. Used with permission.

Table 2. Morphometrics for Townsend’s big-eared bat and two morphologically similar species in USDA Forest Service Region 2.

<table>
<thead>
<tr>
<th>Species</th>
<th>Ear Length (mm)</th>
<th>Forearm Length (mm)</th>
<th>Total Length (mm)</th>
<th>Mass (g)</th>
<th>Reference</th>
</tr>
</thead>
<tbody>
<tr>
<td>(Corynorhinus townsendii)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>(Euderma maculatum)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Pallid bat</td>
<td>21-37</td>
<td>45-60</td>
<td>92-135</td>
<td>14-29</td>
<td>Hermanson and O’Shea (1983)</td>
</tr>
<tr>
<td>(Antrozous pallidus)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

by having smaller ears and a larger body. In addition, the dorsal fur of pallid bats is darker at the tips than at the base, whereas Townsend’s big-eared bat has fur with light tips and dark base. Also unlike Townsend’s big-eared bats, pallid bats generally roost in rock crevices. Although pallid bats are known to use caves or mines as day roosts (Hermanson and O’Shea 1983, Ports and Bradley 1996) and hibernacula (Nagorsen and Brigham 1993), they are often found in crevices within the structure, whereas Townsend’s big-eared bats does not use crevices (Barbour and Davis 1969).

Echolocation

The echolocation of Corynorhinus townsendii (Figure 3) is well suited to the bat’s hawking/gleaning mode of foraging flight. Townsend’s big-eared bat uses a broadband, frequency modulated (FM) call that is most effective for short-range target detection amongst background clutter. This type of echolocation would be expected of bats like C. townsendii that are capable of slow, highly maneuverable flight (Norberg and Rayner 1987) and that forage around or directly from vegetation. The calls are characterized by FM pulses that sweep downward from a maximum frequency of about 40 kHz to a minimum frequency of about 30 kHz. Each pulse comprises a fundamental harmonic and one or more secondary harmonics. The duration (and therefore the bandwidth) of the fundamental harmonic of the echolocation pulse is short, relative to other insectivorous bats. However, C. townsendii makes greater use of secondary harmonics, thereby increasing.
Figure 3. Sonogram of the echolocation call of Townsend’s big-eared bat 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. Note that the upper set of pulses represents a secondary harmonic of the call, which has less energy (i.e., is quieter and less readily detected) than the fundamental harmonic. Because Anabat detectors usually record only the fundamental harmonic for most species of bats, the presence of the secondary harmonic can be used to identify Townsend’s big-eared bat. However, caution and experience are necessary to differentiate secondary harmonics from call echoes deflected from flat water or the presence of multiple bat calls, as these phenomena yield call files that look similar. Townsend’s big-eared bat produces relatively low intensity calls (i.e., quieter) compared to some other species of bats, and may be under-represented in acoustic surveys as a result.
the effective bandwidth of the call (Fenton 1982). The echolocation calls of C. townsendii are of relatively low intensity (i.e., not very loud), limiting somewhat the effectiveness of using acoustic detectors to confirm their presence.

Although acoustic tools to monitor echolocation calls of foraging bats have gained popularity and enjoy widespread use, specialized skills and knowledge are required to correctly interpret the results from surveys employing these tools. We address this issue in more detail in the Tools and practices section below.

**Systematics**

Townsend’s big-eared bat is in class Mammalia, order Chiroptera, family Vespertilionidae, and tribe Plecotini. In addition to the genus Corynorhinus, Plecotini contains the New World genera Euderma and Idionycteris and the Old World genera Barbastella, Otonycteris, and Plecotus.

Townsend’s big-eared bat has been alternately classified as Plecotus or Corynorhinus. Based on phylogenetic evidence (Frost and Timm 1992, Tumlinson and Douglas 1992) that supports Allen’s (1865) use of Corynorhinus rather than Plecotus (Cooper 1837, Handley 1959), C. townsendii is the currently accepted and genetically supported scientific binomial (Bogdanowicz et al. 1998) for Townsend’s big-eared bat. Prior to Handley’s (1959) revision of New World plecotines, C. townsendii was sometimes referred to as C. rafinesquii (e.g., Dalquest 1947, Pearson et al. 1952).

Five subspecies of Corynorhinus townsendii are recognized: C. townsendii australis, C. townsendii pallescens, and C. townsendii townsendii in the western United States and Mexico, and C. townsendii ingens and C. townsendii virginianus in the Ozark and Appalachian regions, respectively (Kunz and Martin 1982, Piaggio and Perkins 2005). We refer to the latter two subspecies as eastern subspecies throughout this document. The western subspecies may interbreed where they co-occur, but the two eastern populations are geographically isolated and do not interbreed.

Townsend’s big-eared bats in Region 2 are generally considered to be Corynorhinus townsendii pallescens (e.g., Pierson et al. 1999). However, recent molecular work suggests that both C. townsendii pallescens and C. townsendii townsendii occur broadly in Region 2 (Figure 4) and that populations in Kansas are C. townsendii australis (Piaggio and Perkins 2005). Until and if such time as subspecies distinctions and associated ranges carry statutory implications, the occurrence of interbreeding (Pierson et al. 1999) and inherent morphological and ecological similarities render distinctions tenuous from a management perspective. Hence, for the purposes of this document, we refer to Townsend’s big-eared bats in Region 2 simply as C. townsendii.

### Distribution and abundance

*Corynorhinus townsendii* is distributed broadly throughout western North America, and it occurs in two disjunct, isolated populations in the central and eastern United States (Figure 4). In the West, this species’ range extends from the Pacific coast north to southern British Columbia, south to central and southern Mexico and the Baja Peninsula. The eastern-most extent of the western range includes the Black Hills of South Dakota and Wyoming, a small region of south-central Kansas, and western portions of Texas and inland eastern Mexico.

In Region 2, the most widespread distributions of *Corynorhinus townsendii* occur in Colorado and Wyoming (Table 3, Figure 5). Distribution of the bat elsewhere in Region 2 is relatively restricted, reflecting the eastern limit of the species’ range. This eastward limitation is likely driven by the same forces that shape the bat’s regional and local distribution. Because of its narrow roosting preferences, local distribution of Townsend’s big-eared bat tends to be restricted by the presence of suitable roosting habitat (i.e., primarily caves and mines, but also lava tubes, abandoned buildings, and large tree hollows) (Kunz and Martin 1982). At the state level, data on known occurrences may be complemented with projections of where *C. townsendii* is likely to occur. To that end, GAP analyses for *C. townsendii* and associated predictive distribution maps are available for Colorado, South Dakota, and Wyoming (Figure 6, Figure 7, Figure 8). The reader should note, however, that although these predictive maps have some value for identifying areas likely to support Townsend’s big-eared bat by highlighting areas with high potential for occurrence, they cover relatively large areas and rely on digital cover data that are coarse in detail. Thus, these maps should be considered a rough, “first guess” of potential distribution at about the time they were created and subject to the constraints of input data. Details about how distributions were predicted can be found in each state’s GAP reports (available through the National Gap Analysis web page: http://www.gap.uidaho.edu/).
Figure 4. Range-wide and USDA Forest Service Region 2 (outlined in bold) distribution of Townsend’s big-eared bat (*Corynorhinus townsendii*). Inferred distribution of the three western subspecies based on DNA analysis (Piaggio and Perkins 2005). The large westernmost distribution (1) corresponds to *C. townsendii townsendii*. The central distribution (2) represents *C. townsendii pallescens*, and the southernmost distribution (3) represents *C. townsendii australis*. Note that these distributions of subspecies differ from those based on morphological characteristics suggested by Handley (1959), who limited *C. townsendii townsendii* to the Pacific coast. According to the distribution above, *C. townsendii pallescens* is more limited in distribution than previously thought, whereas *C. townsendii townsendii* is more widespread. Also according to this distribution, all 3 western subspecies are predicted to occur in Region 2, with *C. townsendii townsendii* occurring throughout Wyoming and in South Dakota, *C. townsendii pallescens* occurring in central and southwestern Colorado, and *C. townsendii australis* occurring in Kansas. The eastern populations (4 and 5) are *C. townsendii ingens* and *C. townsendii virginianus*, respectively. Adapted from Piaggio and Perkins (2005).

Table 3. Distribution by county of Townsend’s big-eared bat in USDA Forest Service Region 2. Data compiled from a variety of sources including state natural heritage databases and state wildlife division publications.

<table>
<thead>
<tr>
<th>State</th>
<th>Counties of Occurrence</th>
</tr>
</thead>
<tbody>
<tr>
<td>Kansas</td>
<td>Barber, Comanche, Kiowa</td>
</tr>
<tr>
<td>Nebraska</td>
<td>Sheridan†</td>
</tr>
<tr>
<td>South Dakota</td>
<td>Custer, Fall River, Harding, Lawrence, Meade, Pennington</td>
</tr>
<tr>
<td>Wyoming</td>
<td>Albany, Bighorn, Carbon, Converse, Crook, Fremont, Goshen, Hot Springs, Johnson, Laramie, Natrona, Niobrara, Park, Platte, Sheridan, Sweetwater, Washakie</td>
</tr>
</tbody>
</table>

†Known only from a single male specimen found hanging on a screen door in 1972. Unless other confirmed sightings exist, this sighting may be considered anomalous.
Figure 5. Range map (tan polygon) and known occurrences (blue dots) for Townsend’s big-eared bat in Region 2. Green polygons represent national forests and grasslands. Data on occurrences are from the Wyoming Natural Diversity Database (WYNDD Database 2001).

Figure 6. Predicted distribution of Townsend’s big-eared bat in Colorado. Light green and dark green areas indicate areas of known or likely occurrence. Light tan and dark tan areas indicate areas of unlikely or no known occurrence. Image from Colorado Gap Analysis Project (Shrupp et al. 2000).
Figure 7. Known and predicted distribution of Townsend’s big-eared bat in South Dakota. Image from South Dakota Gap Analysis Project (Smith et al. 2002).

Figure 8. Predicted potential distribution of Townsend’s big-eared bat in Wyoming. Blue indicates species expected to be present in primary habitat. Tan indicates species expected to be present in secondary habitat. White indicates species not present. Note that expected distribution is overestimated as modeling was based on vegetative coverages, but important roosting habitat (caves, mines and buildings) are not mapped at this scale. Image from Wyoming Gap Analysis Project (Merrill et al. 1996).
Most authors note that Townsend’s big-eared bat is not very abundant anywhere in its range (Barbour and Davis 1969, Kunz and Martin 1982). This relative rarity is often attributed to patchy distribution and limited availability of suitable roosting habitat, but it may also reflect intrinsic limitations in the species’ life history (Humphrey and Kunz 1976). The generalization of modest abundance appears to hold within Region 2 as well. For instance, recent surveys at abandoned mines and caves in Colorado have revealed 14 maternity roosts, most of which contained fewer than 50 individuals (K. Navo personal communication 2003), and a survey of 99 caves in Colorado found no more than six Corynorhinus townsendii individuals in any one cave (Siemers 2002). However, Townsend’s big-eared bat can be locally abundant, as one of the largest colonies of hibernating C. townsendii in the western United States (estimated at 800 to 900 individuals) is found in the Black Hills of South Dakota (Choate and Anderson 1997).

No population estimates are available for Corynorhinus townsendii in the West, and indeed, reliable estimates of population densities of bats are notoriously difficult to obtain and are often logistically impractical (O’Shea and Bogan 2003; also see our discussion below in Tools and practices section). The availability and quality of roosting and foraging habitat, local environmental conditions, natural population fluctuations, and the interactions of all these factors ultimately influence the number of bats in a given area at a given time.

To our knowledge, the following are the only published estimates of density for Corynorhinus townsendii in the West, and although crude, they provide our only insight into local population densities. Humphrey and Kunz (1976) estimated that Townsend’s big-eared bats achieved densities of one bat per 38 ha (94 acres) on a small tract in Kansas and Oklahoma, and Pearson et al. (1952) estimated densities of one per 126 ha (311 acres) and per 170 ha (420 acres) in northern California and on Santa Cruz Island off the coast of California, respectively. However, these estimates must be considered cautiously and should not be extrapolated to other areas. The estimate from northern California is likely not reliable owing to unjustified and untested assumptions. Moreover, each represents a snapshot in time of populations at the three locations, and thus they are best suited as baseline data for those locations.

The eastern subspecies, federally listed as endangered (U.S. Fish and Wildlife Service 1979), have received more rigorous monitoring of populations. As of 2001, numbers of Townsend’s big-eared bats in Oklahoma and Arkansas (Corynorhinus townsendii ingens) were estimated at fewer than 1700 individuals (Harvey and Redman 2002). Numbers of Virginia big-eared bats (C. townsendii virginianus) as of 2000 were estimated to be 18,442 individuals (Currie 2000).

Population trend

A general decline in the numbers of cave-dwelling species of bats in North America was recognized as early as the 1950’s, with reports of declines continuing through the 1960’s and early 1970’s (Mohr 1953, Manville 1962, Booth 1965, Henshaw 1972). Despite this, detailed long-term data on which to base estimates of population trends for many species of bats are generally lacking (Fenton 2003). However, the limited survey data available for Corynorhinus townsendii at a few known nursery sites and hibernacula in the West have lead to speculation of a general decline in numbers. For example, surveys for C. townsendii at historic roost sites in California from 1987 to 1991 indicated a 52 percent reduction in numbers of maternity colonies and a 55 percent decline in number of animals (Pierson and Rainey 1998). In Oregon, half of the known colonies were believed to have been either extirpated or had experienced substantial decline in numbers (Pierson et al. 1999).

Activity and movement patterns

The daily and annual activity patterns of Corynorhinus townsendii mirror those of most other north-temperate species of bats and are dictated largely by daily cycles of light and dark and seasonal cycles of warm and cold. Bats of the north temperate regions of the world are active primarily during the summer months when insect prey is available and warm temperatures facilitate cost-efficient thermoregulation. Bats avoid winter food scarcity either by hibernating or by migrating to warmer climes. In areas where winter temperatures predominantly remain below freezing, bats are rarely seen outside the hibernation roost during winter.

During the summer months, bats are most active during the crepuscular periods of the day. During the daylight hours, bats typically remain secluded in the day roost (Barbour and Davis 1969), where they are generally inactive. As twilight approaches and darkness falls, bats emerge from their roosts to forage for insects and drink water. Foraging activity by bats generally peaks 1 to 2 hours after sunset, remains at low levels throughout the night, and often exhibits another smaller
peak just before sunrise. The drop-off in foraging activity after the initial peak is correlated with a decrease in aerial activity by insects. During this period, bats use night roosts to rest and digest food (Perlmeter 1995). Often, a second smaller peak in activity before sunrise is seen, and it may reflect bats commuting to day roosts while opportunistically exploiting aerially-active insects (Hayes 1997). Lactating females typically forage for longer periods, probably to meet increased energetic demands, and early in lactation females return to the roost several times per night to nurse their young (e.g., Clark et al. 1993).

Harsh winter conditions coupled with lack of insect prey mean that bats face increased thermoregulatory costs at a time when the source of energy for thermoregulation is reduced or absent. Many bats solve the problem of overwinter survival through the use of deep physiological torpor known as hibernation during which the animal allows body temperature to fall to within 1 to 2 °C of ambient conditions (Schmidt-Nielsen 1997). Hibernation leads to substantial reductions in energy expenditure, and it allows animals to survive many months without access to food (Humphries et al. 2002).

**Diel cycle**

Townsend’s big-eared bat is reported to be a late-flier relative to other bats (Kunz and Martin 1982). They may begin flying within the roost up to 30 minutes before sunset (Clark et al. 1993), but typically, they leave the roost from 45 to 60 minutes after sunset (Clark et al. 1993, Dobkin et al. 1995, Fellers and Pierson 2002). Townsend’s big-eared bats may fly directly to foraging sites after emergence without foraging en route (Adam et al. 1994), or they may forage immediately upon emergence near the roost for a few hours before moving to foraging sites farther from the roost (Dobkin et al. 1995). Lactating females appear to forage all night although they return to the day roost to nurse the young several times. Males and non-lactating females tend to show a bimodal pattern of foraging activity, with the largest peak occurring during the first 1 to 2 hours following sunset and another smaller peak just prior to sunrise (Pierson et al. 1999). After the initial feeding period, Corynorhinus townsendii selects a night roost, often in a warm cave or cave analog, to rest and digest food. Night roosts tend to be in different structures than day roosts (Pierson et al. 1999). In general, lactating female bats appear to make less use of night roosts than other bats (Barclay 1982) because they must return to the day roost during the night to nurse their young (Kunz 1974, Barclay 1982, Racey and Swift 1985, Waldien and Hayes 2001). Townsend’s big-eared bats appear to follow this pattern as well (Cockrum and Cross 1964, Clark et al. 1993, Adam et al. 1994).

Moon phase is thought to affect foraging activity patterns in bats, with bats hypothesized to be less active on bright, moonlit nights (e.g., Morrison 1978, Usman et al. 1980). However, moon brightness did not affect flight activity in Corynorhinus townsendii ingens in Oklahoma (Clark 1991), and recent evidence suggests that activity levels for bats are not correlated with lunar phase or ambient light levels (Hecker and Brigham 1999, Karlsson et al. 2002). Although definitive effects of moonlight on foraging behavior in bats remain to be shown, it is highly unlikely that Townsend’s big-eared bat chooses to forgo or reduce foraging during the period of each month when the moon is large. If moon phase affects the foraging behavior of Townsend’s big-eared bat at all, a likely scenario is that the bat spends more time near and within vegetation, perhaps as a predator avoidance strategy (e.g., Reith 1982), but more likely as it follows shifting distributions of insects. For instance, Hecker and Brigham (1999) showed that foraging activity of insectivorous bats was greater within and above forest canopy on moonlit nights, a result that is non-congruent with predator avoidance behavior, but that is likely a response to shifts in insect (particularly lepidopteran) activity (Hecker and Brigham 1999 and references therein). Since it is probable that such shifts in foraging patterns reduce the success rate of captures at ground-based mist-nets (the most typical deployment of mist-nets), the impression of lower levels of activity on moonlit nights is probably misleading and underscores one of several inherent difficulties in accurately assessing movement patterns by insectivorous bats (see also our discussion below in Tools and methods section).

**Annual cycle**

Like most temperate-zone bats, Corynorhinus townsendii escapes the harsh conditions and lack of prey during winter by hibernating. Hibernation occurs from early fall through early spring. Movements toward hibernacula begin in late summer (Pearson et al. 1952) after dissolution of maternity colonies, and Townsend’s big-eared bats typically begin to arrive at hibernacula in October. Males often arrive before females (Pearson et al. 1952). In California, Kansas, and Oklahoma, maximum numbers were present in January (Pearson et al. 1952, Humphrey and Kunz 1976). Movement to hibernacula may require northward or elevational migration to find roosts with suitable temperatures for hibernation (Pierson et al. 1999).
Available evidence suggests that *Corynorhinus townsendii* use interim roosts (to which they show little fidelity) while moving between summer and winter grounds (Pearson et al. 1952, Dobkin et al. 1995). Interim roosts appear to serve as “staging grounds” and may foster commingling of the sexes for breeding, serve to apprise juveniles of the location of hibernacula, or promote synchronous arrival of pregnant females at maternity roosts.

Habitat

*General requirements*

Townsend’s big-eared bat is unequivocally associated with areas containing caves and cave-analogs for roosting habitat. Beyond the constraint for cavernous roosts, habitat associations become less well defined. Generally, Townsend’s big-eared bats are found in the dry uplands throughout the West, but they also occur in mesic coniferous and deciduous forest habitats along the Pacific coast (Kunz and Martin 1982).

Townsend’s big-eared bat requires spacious cavern-like structures for roosting (Pierson et al. 1999) during all stages of its life cycle. Typically, they use caves and mines, but *Corynorhinus townsendii* have been noted roosting in large hollows of redwood trees (Fellers and Pierson 2002), in attics and abandoned buildings (Dalquest 1947, Fellers and Pierson 2002), in lava tubes (Handley 1959, Hinman and Snow 2004), and under bridges (Keeley 1998, Adam and Hayes 2000, Fellers and Pierson 2002). In Utah, 85 percent of surveyed caves and 21 percent of surveyed mines were used as day roosts in summer (Sherwin et al. 2000a), and 27 percent of all structures surveyed showed signs of occupancy (Table 4). In coastal California, five of six known maternity colonies were in old buildings; the sixth was in a cave-like feature of a bridge (Fellers and Pierson 2002).

A combination of internal complexity and dimensions, and size of the openings appear to drive Townsend’s big-eared bat use of particular caves and mines as roost structures. These parameters likely reflect the diversity of internal roosting conditions that a structure is likely to offer bats. For instance, a structure with greater internal complexity and dimensions (e.g., natural cave) likely affords a greater variety of temperature and humidity regimes, and hence more roosting opportunities for bats as roosting requirements change (e.g., early pregnancy versus lactation). Size of opening may influence the accessibility of predators to roosts. Perhaps more importantly, though, the size of openings tends to regulate and maintain temperature and humidity profiles within roosts via air exchange

### Table 4. Occupied roosts by elevation zones and habitat types for Townsend’s big-eared bat in Utah. Adapted from Sherwin et al. (2000a).

<table>
<thead>
<tr>
<th>Elevation</th>
<th>Number of Roosts Surveyed (% of Total Surveyed)</th>
<th>Number of Roosts Occupied (% of Total Occupied)</th>
<th>Percentage of Total Roosts Surveyed That Were Occupied</th>
</tr>
</thead>
<tbody>
<tr>
<td>&lt;1700 m</td>
<td>75 (10.5)</td>
<td>53 (70.6)</td>
<td>7.4</td>
</tr>
<tr>
<td>1701-2000 m</td>
<td>139 (19.4)</td>
<td>79 (56.8)</td>
<td>11.0</td>
</tr>
<tr>
<td>2001-2300 m</td>
<td>115 (16.1)</td>
<td>36 (31.3)</td>
<td>5.0</td>
</tr>
<tr>
<td>2301-2600 m</td>
<td>123 (17.2)</td>
<td>27 (21.9)</td>
<td>3.8</td>
</tr>
<tr>
<td>2601-2900 m</td>
<td>142 (19.9)</td>
<td>0 (0.0)</td>
<td>0.0</td>
</tr>
<tr>
<td>2901-3200 m</td>
<td>92 (12.9)</td>
<td>1 (1.1)</td>
<td>0.1</td>
</tr>
<tr>
<td>3201-3500 m</td>
<td>29 (4.0)</td>
<td>0 (0.0)</td>
<td>0.0</td>
</tr>
<tr>
<td>Total</td>
<td>615</td>
<td>14.3</td>
<td>27.4</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Habitat Type</th>
<th>Number of Roosts Surveyed (% of Total Surveyed)</th>
<th>Number of Roosts Occupied (% of Total Occupied)</th>
<th>Percentage of Total Roosts Surveyed That Were Occupied</th>
</tr>
</thead>
<tbody>
<tr>
<td>Riparian</td>
<td>18 (2.5)</td>
<td>2 (0.11)</td>
<td>0.3</td>
</tr>
<tr>
<td>Sagebrush-grass steppe</td>
<td>156 (21.8)</td>
<td>69 (44.2)</td>
<td>9.6</td>
</tr>
<tr>
<td>Juniper woodland</td>
<td>118 (16.5)</td>
<td>76 (64.4)</td>
<td>10.6</td>
</tr>
<tr>
<td>Mountain brush</td>
<td>100 (14.0)</td>
<td>41 (41.0)</td>
<td>5.7</td>
</tr>
<tr>
<td>Aspen</td>
<td>170 (23.8)</td>
<td>5 (0.03)</td>
<td>0.7</td>
</tr>
<tr>
<td>Mixed conifer</td>
<td>153 (21.4)</td>
<td>3 (0.02)</td>
<td>0.4</td>
</tr>
<tr>
<td>Total</td>
<td>1230</td>
<td>60.54</td>
<td>27.4</td>
</tr>
</tbody>
</table>
between surface and subterranean habitats (Richter et al. 1993, Roebuck et al. 1999).

Most maternal roosts in California had entrances that were at least 15 cm (6 inches) high and 31 cm (12 inches) wide, and heights of roosts ranged from 2.4 to 4.9 m (8 to 16 ft.), with an area large enough to permit flight (Pierson and Rainey 1998). In Utah, bats were more likely to occupy caves and mines with single, low entrances that did not exceed 1.5 m (5 ft.) in height, and maternal colonies tended to be located in larger, more complex sites that had multiple openings and were generally subject to minimal human disturbance (Sherwin et al. 2000b). Other external and internal characteristics (e.g., aspect and width of opening, tunnel length, and amount of internal airflow) were not associated with probability of use in summer (Sherwin et al. 2000b). Similar results were reported for roosts in Nevada and Utah (Sherwin et al. 2003) and the Black Hills of South Dakota (Tigner and Dowd Stukel 2003).

Throughout its western range, Corynorhinus townsendii roosts in a variety of vegetative communities, and at a range of elevations (Table 5), and there appears to be little or no association between local surface vegetative characteristics and selection of particular subsurface roosts in either eastern or western populations (Wethington et al. 1997, Sherwin et al. 2000b, 2003). This suggests that the bats select roosts based on internal characteristics of the structure rather than the surrounding vegetative community. In Colorado, Townsend’s big-eared bat is reported to occur across all four of Colorado’s ecoregions (i.e., Wyoming Basin, Colorado Plateau, Southern Rocky Mountains, Central Shortgrass Prairie) (Ellison et al. 2003a) and in at least five community types (i.e., Saxicoline brush, sagebrush, semidesert scrub, pinyon-juniper woodland, ponderosa pine woodland) (Ellison et al. 2003a). Because Townsend’s big-eared bat has also been reported to roost at elevations approaching 3048 m (10,000 feet) in Colorado (Siemers 2002), we surmise that this bat also uses roosts in lodgepole pine and subalpine spruce-fir communities, at least in the southern Rockies. Association with vegetative communities in Colorado reflects the distribution of roosting habitat in these communities and does not

### Table 5. General roosting habitat associations and characteristics for Townsend’s big-eared bat in the western United States.

<table>
<thead>
<tr>
<th>Location</th>
<th>Vegetative Community</th>
<th>Roost Structures</th>
<th>Elevation Range</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Colorado</td>
<td>Saxicoline brush, sagebrush, semidesert scrub, pinyon-juniper woodland, ponderosa pine woodland, montane forest and subalpine forest</td>
<td>Caves and mines</td>
<td>1866-3014 m (6122-9890 ft.)</td>
<td>Ellison et al. (2003a), Siemers (2002)</td>
</tr>
<tr>
<td>California and Nevada</td>
<td>Mojave and Great Basin desert scrub, pinyon-juniper woodland, bristlecone-limber pine forest</td>
<td>Caves and mines</td>
<td>1372-3188 m (4500-10,460 ft.)</td>
<td>Szcewczak et al. (1998)</td>
</tr>
<tr>
<td>Utah</td>
<td>Sagebrush-grass steppe, juniper woodlands, mountain brush</td>
<td>Caves and mines</td>
<td>1350- &gt;2600 m (4430- &gt;8500 ft.)</td>
<td>Sherwin et al. 2000b</td>
</tr>
<tr>
<td>Central California and Washington</td>
<td>Coastal lowlands, cultivated valleys, hills with mixed vegetation</td>
<td>Not applicable</td>
<td>Not applicable</td>
<td>Handley (1959)</td>
</tr>
</tbody>
</table>
Maternity roosts comprise Table 6, areas. Temperatures inside hibernacula are reported to the entrance to be in relatively cold, well-ventilated spaces. Internal conditions appear to drive roost selection more than surface conditions do (Sherwin et al. 2000b). Temperature and humidity are thought to play important roles, and these variables depend on the depth and complexity of the structure and airflow. Bats appear to prefer roosts with low to moderate levels of airflow, likely because airflow helps to keep roosts from getting too warm or too cold. Internal temperature, which dictates energy expenditure by bats, appears to drive the selection of maternity roosts. For example, maternity roosts of Corynorhinus townsendii in California ranged between 18 and 30 ºC (64 and 86 ºF) and were significantly lower than those in Colorado. Hibernacula are generally viewed as housing large aggregations of bats that can number into the 10’s or 100’s of thousands (Barbour and Davis 1969), but abundance of hibernating Corynorhinus townsendii appears to be much lower (Table 6). Physical and abiotic requirements for hibernacula are restrictive, and this may lead to relatively few suitable hibernation sites. For instance, in some parts of the range, caves used for summer roosts are too warm for successful hibernation (Graham 1966), and bats likely migrate in latitude or elevation to suitable sites that are probably shared with groups from other areas. Thus, suitable hibernacula may harbor denser aggregations of bats than summer roosts (Table 6). Because mating occurs at hibernacula both before and after the onset of hibernation, and because these roosts likely house bats from a wide geographic area, hibernacula may play an important role in maintaining genetic diversity among western populations of Townsend’s big-eared bats, as is the case for other species of bats (Burland et al. 2001).

Because hibernating bats are physically inert due to their highly reduced metabolic rate, they are incapable of escaping direct disturbance or outright aggression in any temporally meaningful way. Disturbance may lead to unnecessary arousal from hibernation and concomitant expenditure of crucial energy reserves (Thomas 1995). If disturbance leads to abandonment, then the expense of flight and of locating alternate suitable hibernacula markedly increases the risks to which the bats are subjected.

Maternity roosts: Maternity roosts comprise reproductive females and their young of the year. Adults males are occasionally found in maternity roosts, often early in the season, but they appear not to be part of the social unit as they may be found roosting apart from the group. Mating can be ruled out as a reason for the presence of males since copulation cannot commence until late summer. Considering the high degree of inter- and intra-season fidelity exhibited by maternity colonies to particular roosts, and the relatively low annual reproductive rate of Corynorhinus townsendii, maternity roosts are also considered to have high conservation value.

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Internal temperature, which dictate...
Table 6. Summary of abundance of Townsend’s big-eared bat in the western United States based on capture records and survey observations.

<table>
<thead>
<tr>
<th>Method of Capture or Observation</th>
<th>Number Captured or Observed</th>
<th>Roost Type or Season Observed</th>
<th>Location</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>Internal survey</td>
<td>~100 + approx. same number of juveniles</td>
<td>Not applicable</td>
<td>Senator Mine, California</td>
<td>Howell (1920)</td>
</tr>
<tr>
<td>Mist-netting over water, Cave survey</td>
<td>43 (3rd most abundant)</td>
<td>Summer</td>
<td>Badlands National Park, South Dakota</td>
<td>Bogan et al. (1996)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>33 (3rd most abundant)</td>
<td>Early &amp; late summer</td>
<td>Colorado (Karst regions)</td>
<td>Siemers (2002)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>85 adult females (avg)</td>
<td>Maternity</td>
<td>Marin Co., California</td>
<td>Pearson et al. (1952)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>60 adult females (avg)</td>
<td>Maternity</td>
<td>Napa Co., California</td>
<td>Pearson et al. (1952)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>111-201 (avg = 144)</td>
<td>Hibernaculum</td>
<td>Shasta Co., California</td>
<td>Pearson et al. (1952)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>22-93 (avg = 51)</td>
<td>Hibernaculum</td>
<td>Shasta Co., California</td>
<td>Pearson et al. (1952)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>30</td>
<td>Hibernaculum</td>
<td>Siskiyou Co., California</td>
<td>Pearson et al. (1952)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>23-183 (avg = 103)</td>
<td>Hibernaculum</td>
<td>Napa Co., California</td>
<td>Pearson et al. (1952)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>~90</td>
<td>Not applicable</td>
<td>Spring Cave, Colorado</td>
<td>Finley et al. (1983)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>46-148</td>
<td>Hibernaculum</td>
<td>Torgac Cave, New Mexico</td>
<td>Jagnow (1988)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>110 (including juveniles)</td>
<td>Maternity</td>
<td>Northern Black Hills, South Dakota</td>
<td>Tigner and Dowd Stukel (2003)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>7-37 (avg = 26; n = 3)</td>
<td>Hibernaculum</td>
<td>Northern Black Hills</td>
<td>Tigner and Dowd Stukel (2003)</td>
</tr>
<tr>
<td>Internal survey</td>
<td>~300</td>
<td>Hibernaculum</td>
<td>Jewel Cave National Monument, South Dakota</td>
<td>Tigner and Dowd Stukel (2003)</td>
</tr>
</tbody>
</table>

\[a\] Includes males and females. Males were always more numerous. Surveys occurred over 3 winters.

\[b\] Includes males and females. Females were always more numerous. Surveys occurred over 2 winters.

Warmer than random structures (Pierson and Rainey 1998). However, during early pregnancy, maternity colonies appeared to choose cooler sites (either in the same roosts or in different roosts) than during late pregnancy and lactation (Pierson and Rainey 1998) when female’s energetic demands are greatest (Kurta et al. 1989). By choosing cooler sites during early pregnancy, when energetic costs are lower, females can save energy by using torpor.

Bachelor roosts: As the name suggests, these roosts generally house groups of adult males during the non-mating season. Bachelor roosts likely have less constrained thermal requirements than maternity roosts and hibernacula owing to the generally accepted flexibility of males to utilize more frequent and deeper bouts of torpor as a means of energy savings. However, while conferring energetic savings, torpor also exerts some potential costs such as decreased predator avoidance. Thus, adult males may select bachelor roosts based on disturbance levels rather than specific thermal requirements. If so, then bachelor colonies may roost in dangerous (to humans) and generally inaccessible caves or mines that likely receive little disturbance. As with other roost types, efforts to protect these structures from disturbance and destruction will benefit Townsend’s big-eared bats.

Foraging habitat

Townsend’s big-eared bat has been noted foraging in a wide variety of habitats (Pierson et al. 1999) throughout its western range, and this may reflect the need to roost where structures are available as opposed to within a particular vegetative zone. Given its wing morphology, which permits slow maneuverable flight and the ability to hover and glean insects from vegetation (Norberg and Rayner 1987), Corynorhinus townsendii is expected to forage primarily in and near vegetation, and to engage in little if any of the open-air hawking that is characteristic of swift-flying species such as hoary bats (Lasiurus cinereus). Thus, suitable foraging...
habitat for *C. townsendii* will likely be a heterogeneous mosaic of forested and edge habitats, including riparian zones, which are also used for commuting and drinking (e.g., Fellers and Pierson 2002). Areas with substantial beaver activity enhance the quality of foraging habitat by increasing ecosystem productivity (Naiman et al. 1986), providing gaps in the forest canopy, providing small, quiet ponds for drinking, and causing an increase in insect activity. Individuals or colonies appear to favor specific foraging locations to which they show a high degree of fidelity and where they forage extensively, usually amongst foliage of trees and shrubs and along forest edges (Clark et al. 1993, Adam et al. 1994, Ports and Bradley 1996, Fellers and Pierson 2002). Female *Corynorhinus townsendii* in Nevada tended to forage in forested areas, including pinyon-juniper, mountain mahogany, mixed-fir, and riparian deciduous habitats, but they appeared to avoid foraging in open sagebrush/grassland steppe (Bradley 1996). In California, both males and females foraged along the edges of riparian vegetation dominated by Douglas-fir, California bay, and willow species, but they also avoided open grasslands both when traveling and foraging (Fellers and Pierson 2002). In Oregon, bats foraged in sagebrush shrubsteppe and in open ponderosa pine woodlands, with little foraging activity in more densely forested areas (Dobkin et al. 1995).

Characteristics of foraging habitat for the eastern subspecies appear to be similar to those observed in the West, with the exception that in some cases, bats in the East appeared to forage more in open areas. Townsend’s big-eared bats in West Virginia foraged over hayfields early in the evening but moved to forest habitat later in the night (Pierson et al. 1999). In Kentucky, Townsend’s big-eared bats foraged along cliffs and within forested habitats, but they avoided open areas while traveling and foraging (Adam et al. 1994). In Oklahoma, *Corynorhinus townsendii* foraged over pastures, crops, and native grasslands, as well as along intermittent streams, but in all cases, they foraged near wooded edges (Clark et al. 1993). Proximity to vegetation in general, and especially while foraging in more open areas, appears to be a consistent pattern; *C. townsendii* in California showed close association with scattered trees and shrubs while foraging in more open areas (Fellers and Pierson 2002).

**Seasonal and life history shifts**

Townsend’s big-eared bat uses caves and cave-like structures during all parts of its life cycle. Individuals may move within and among roosts during summer and winter (Genter 1986, Sherwin et al. 2003). During hibernation, these bats commonly change position within a hibernaculum or move to a nearby roost, presumably to find temperatures that are more suitable. Roost movement in the summer likely occurs for the same reason.

Townsend’s big-eared bat is a relatively sedentary species and appears not to engage in long distance migrations. Reported movement between summer roosts and hibernacula ranges from 3.1 to 64 km (2 to 40 miles) (Kunz and Martin 1982). Maximum-recorded distances moved vary by geographic location. In California, maximum known distance traveled to hibernaculum is 32 km (20 miles) (Pearson et al. 1952), and in Kansas, movements of 40 km (25 miles) are known (Humphrey and Kunz 1976). Big-eared bats in West Virginia and Kentucky are known to have moved 64 km (40 miles) to hibernacula (Barbour and Davis 1969). The greater distances observed in the eastern subspecies may reflect the relatively limited number of hibernation roosts in the East (Pierson et al. 1999). As with other species of bats, *Corynorhinus townsendii* appears to engage in elevational migrations between seasons, probably to find roosts with conditions necessary for various life stages. In the Black Hills, *C. townsendii* hibernates at an elevation of approximately 1600 m (5250 ft.), but captures of females during summer are known from elevations below 1100 m (3600 ft.) (Cryan et al. 2000). Similarly, maternity colonies in the Black Hills are known from elevations below 1300 m (4265 ft.) (Cryan et al. 2000).

Based on re-sighting of banded Townsend’s big-eared bats in the Black Hills and in the Great Plains, most bats are re-sighted in the cave in which they were originally banded (Tigner and Dowd Stukel 2003) and/or in nearby caves (Humphrey and Kunz 1976). The two largest hibernating populations known from the Black Hills (i.e., Jewell Cave and a natural cave approximately 9 miles to the north) showed no evidence of common roosting (Tigner and Dowd Stukel 2003). However, because some individuals were unbanded and some of those that were banded may have been missed during surveys, mixing between the roosts cannot be ruled out. Re-sightings of banded bats in the Black Hills at sites other than where the bats were banded demonstrate that movement between roosts occurs, but movement distance is generally low. Of the five re-sightings in different locations, the farthest was 18 km (11 miles) from its original site, and the others were within 4 km (2.5 miles) (Tigner and Dowd Stukel 2003).
Area requirements

Although some general patterns of the size of areas used by Townsend’s big-eared bats can be drawn from knowledge of the area over which some bats have traveled while carrying radio-transmitters, little is understood about the minimum area necessary to support a group of bats. In all likelihood, the minimum required area will vary spatially and temporally, depending on the myriad factors that influence energy costs for bats. Availability of food and water, temperature, precipitation, density of intra- and interspecific competitors, as well as the complex interactions of these factors are all likely to alter area requirements by influencing energy costs for bats.

In general, females appear to increase the distance traveled to foraging sites as the reproductive cycle progresses (Table 7), and females appear to travel farther than males. During the latter stages of reproduction (i.e., lactation and post-lactation), females of the two eastern subspecies appear to increase their foraging areas. In Kentucky, female Corynorhinus townsendii virginianus increased their foraging areas from 60 to 263 ha (148 to 650 acres) between pregnancy and post-lactation; males decreased their foraging areas during the same period (Adam et al. 1994). Males traveled a maximum of 8.4 km (5.2 miles) to foraging areas in Kentucky, whereas females were never found more than 3.65 km (2.25 miles) from roosts (Adam et al. 1994). Clark et al. (1993) observed a four-fold increase (1 to 4.2 km) in median distance traveled to foraging sites by C. townsendii ingens between early lactation and late lactation in Oklahoma, and one female traveled more than 7 km (4 miles) to foraging sites during late lactation. In Nevada, females traveled from 0.8 to 6.4 km (0.5 to 4 miles) from roosts to foraging areas in mid-August, a period that would coincide with late lactation (Bradley 1996). Similar results were reported for C. townsendii during the post-lactation period in coastal central California (mid-September). Foraging areas for females were centered 3.2 ± 0.5 km (2 ± 0.3 miles) from

Table 7. Spatial patterns of foraging by female Townsend’s big-eared bat (Corynorhinus townsendii) in different reproductive stages.

<table>
<thead>
<tr>
<th>Subspecies and Reproductive Period</th>
<th>Location and Timing of Study</th>
<th>Duration of Study</th>
<th>Distance Traveled to Foraging Areas or Size of Foraging Area</th>
<th>Source</th>
</tr>
</thead>
<tbody>
<tr>
<td>C. townsendii</td>
<td>Central Oregon</td>
<td>9 weeks</td>
<td>Range: 5-24 km</td>
<td>Dobkin et al. (1993)</td>
</tr>
<tr>
<td>Early pregnancy</td>
<td>7 April-9 June</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. t. pallescens Post-lactation</td>
<td>East-central Nevada</td>
<td>2 weeks</td>
<td>Range: 0.8-6.4 km</td>
<td>Bradley (1996)</td>
</tr>
<tr>
<td></td>
<td>Mid-August</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. t. townsendii Post-lactation</td>
<td>Coastal central California</td>
<td>10 days</td>
<td>3.2 ± 0.5 km to center of activity areas</td>
<td>Fellers and Pierson (2002)</td>
</tr>
<tr>
<td></td>
<td>Mid-September</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. t. ingens Early lactation – late lactation</td>
<td>8-17 June (early lactation)</td>
<td>7 weeks</td>
<td>(EL): 1.0 (range: 0.5-2.0) km; Foraging area – 89.9 ha (ML): 1.9 (range: 1.1-4.0) km; Foraging area – 156.9 ha (LL): 4.2 (range: 1.1-7.7) km; Foraging area – 65.5 ha</td>
<td>Clark et al. (1993)</td>
</tr>
<tr>
<td></td>
<td>28 June-7 July (mid-lactation)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>17-26 July (late lactation)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>C. t. virginianus Pregnancy – post-lactation</td>
<td>Eastern Kentucky</td>
<td>14 weeks</td>
<td>(PR): Foraging area – 60.5 ha</td>
<td>Adam et al. (1994)</td>
</tr>
<tr>
<td></td>
<td>10-15 May (pregnancy)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td>17-22 June (lactation)</td>
<td></td>
<td>(L): Foraging area – 98.8 ha</td>
<td></td>
</tr>
<tr>
<td></td>
<td>6-11 August (post-lactation)</td>
<td></td>
<td>(PL): 0.74 ± 0.42 km; maximum distance = 3.65 km; Foraging Area – 262.8 ha</td>
<td></td>
</tr>
</tbody>
</table>

1 Distance traveled was not reported in some cases. In these cases, we present the size of foraging areas.
2 Subspecies undifferentiated. Study area was within the zone of intergradation of C. t. pallescens and C. t. townsendii.
3 Reproductive stage not identified. Based on the timing of reproductive stages in other areas, mention of maternity colonies and timing of returns to roosts (between 0300 and 0500 hrs), we make the assumption that the bats were post-lactating.
4 Sample included one nulliparous female.
roosts, and males centered their activity 1.3 ± 0.2 km (0.81 ± 0.1 miles) in California; none of the bats moved more than 10.5 km (6.5 miles) from roosts (Fellers and Pierson 2002). While it is unclear why females travel longer distances to foraging sites as lactation progresses, we may speculate that it is to meet the increased energetic demands of lactation, to allow newly volant young to exploit nearby foraging areas, or because young are able to go longer without nursing, mothers may be less constrained to remain near roosts. Whatever the reason, Townsend’s big-eared bats do not appear to range very far from the roost, even when considering the increased distances traveled by reproductive females. However, there is no good way to determine how far is too far for Corynorhinus townsendii to travel, and it will likely vary from place to place and from season to season. All else being equal, the greater the distance that bats must travel to foraging or drinking sites, the greater will be their energy expenditure.

Landscape context

Of primary importance to animals is the ability to find shelter, food, and water. Most animals have a home range in which these elements are available and familiar to the animal. For example, although female Corynorhinus townsendii in Nevada showed high fidelity to their maternity roost, they displayed familiarity with and casual use of other roosts within their home range (Bradley 1996). The farther an animal must travel to connect these elements, the greater the size of the animal’s home range, and the greater the energetic costs for the animal. Thus, the spatial arrangement and juxtaposition of shelter, food, and water influences an animal’s ability to use a particular area efficiently. Although no studies have specifically addressed the importance of spatial arrangement of various habitat components to C. townsendii, our understanding of what constitutes suitable foraging habitat, combined with knowledge of travel distances and patterns, suggests that foraging and drinking habitat located near roosts and/or connected by vegetated patches or corridors may be necessary to support colonies of C. townsendii.

Townsend’s big-eared bats appear not to travel very far from roost sites to forage or drink. Published estimates of distances traveled from roost to foraging areas report a maximum distance of 10.5 km (6.5 miles), but the distance traveled is usually substantially less. For instance, during the study that recorded the distance of 10.5 km, females traveled on average 3.2 km (2 miles) to foraging sites, and males ventured a mean distance of 1.3 km (0.8 miles) from roosts (Fellers and Pierson 2002). Compared to some species of bats that routinely travel distances several-fold farther (e.g., hoary bats), use of such small areas by Corynorhinus townsendii suggests that landscape context could be a limiting factor. This might be explained by their low wing-loading and their rounded wings, which allow very agile flight, but which also result in relatively inefficient forward flight compared to bats with higher wing-loading and more pointed wing tips (Norberg and Rayner 1987). Given that other similar-sized species with similar wing morphology (e.g., western long-eared bat [Myotis evotis]) also maintain small foraging areas (Waldien and Hayes 2001), energetic costs associated with commuting may constrain C. townsendii and other species of bats that share similar wing morphology to forage near roosts. Whatever the reason, maintaining foraging and drinking habitat within close proximity to roosts may be necessary to allow C. townsendii to meet energetic needs efficiently. If so, an important corollary is that removal or alteration of habitat that reduces the productivity of foraging or drinking areas (e.g., clear-cutting, water diversion, draining wetlands) near roosts may result in extirpation of colonies, whereas activities that increase the value of a site (e.g., selective thinning, water impoundment) will likely benefit bats roosting nearby and may increase the likelihood of long-term persistence of colonies using these sites.

Several authors (e.g., Limpens and Kaptyn 1991, Verboom and Huitema 1997) have noted a propensity for bats in general to use forest-edge habitat, and even to avoid open areas while commuting and foraging, and this appears to be true for Corynorhinus townsendii as well. In Kentucky, male C. townsendii virginianus consistently used an abandoned logging road in forested habitat to commute to foraging areas, and females tended to fly along the edges of cliffs while traveling to foraging areas (Adam et al. 1994). Townsend’s big-eared bats in Nevada and California also used forest edges and other linear landscape elements while commuting (Ports and Bradley 1996, Fellers and Pierson 2002). Use of such linear landscape elements may provide orientation cues, profitable foraging habitat, and, perhaps, shelter from predators of the bats. In addition, movements within vegetated stream corridors or near forest edges may reduce flight costs by buffering bats from windy conditions. Indeed, it is partly because of lower winds that insects tend to collect in such places (Lewis 1970). This may also help to explain why C. townsendii observed crossing open grassland dropped down sharply and flew at a height of about 1 m (3 ft.), whereas they otherwise flew from
10 to 30 m (33 to 100 ft.) above the ground (Fellers and Pierson 2002). In the Rocky Mountains, where natural disturbances maintain patterns of patchy forest habitats (Howe and Baker 2003), *C. townsendii* likely relies on edges and linear landscape elements for foraging and commuting, as they do in other parts of their range. Although gaps in forest canopies and the creation of edge habitat may benefit the bats, too much open space is likely to have negative consequences. Several reports indicate that Townsend’s big-eared bats tend to avoid large openings such as grazed pastureland (reviewed in Pierson et al. 1999).

The connectivity of habitat features can influence how an animal utilizes habitat in their home range. For species that tend to avoid open areas, accessibility to foraging sites may require linear or closely situated habitat patches that they can use while commuting. Consequently, for *Corynorhinus townsendii*, connectivity may be especially important as commuting distance from roosts to foraging or drinking habitat increases. Given that females appear to increase the size of foraging areas and distances commuted as the reproductive season progresses (Clark et al. 1993, Adam et al. 1994), foraging sites that are more distant from roosts will be more accessible if connected by vegetated linear elements (e.g., ravines and stream corridors).

**Food habits**

Reports indicate that *Corynorhinus townsendii* is a moth specialist (e.g., Whitaker et al. 1977, Dalton et al. 1986, Clark 1991, Burford and Lacki 1998), with more than 90 percent of the diet consisting of lepidopterans (reviewed in Pierson et al. 1999). Preferred prey items include small (6 to 12 mm) moths from the families Noctuidae, Geometridae, Notodontidae, and Sphingidae. However, *C. townsendii* appears to forage opportunistically on other prey items (e.g., beetles and flies) as well (Pierson et al. 1999).

In the West, *Corynorhinus townsendii* forage in woodlands, canopy gaps, vegetated stream corridors, and other linear landscape elements but avoid foraging and traveling in open areas and grazed lands (Pierson et al. 1999). Owing to their wing and echolocation morphology, *C. townsendii* are capable of efficient foraging among foliage and of glean ing insects directly from substrates (Norberg and Rayner 1987), and they are predicted to forage primarily in close proximity to foliage and amongst forest canopy. Where foraging patterns by *C. townsendii* have been documented, this association appears to hold (e.g., Bradley 1996, Fellers and Pierson 2002). Individuals or colonies may show high fidelity to particular foraging sites (Bradley 1996, Fellers and Pierson 2002), as well as to routes of travel between roost and foraging grounds (Fellers and Pierson 2002). While commuting, *C. townsendii* tends to follow the same linear features (e.g., stream corridors, forest edges) around which it forages (Fellers and Pierson 2002), and as noted above, connectivity of habitat patches may greatly influence the accessibility of foraging sites to *C. townsendii*.

**Breeding biology**

Pearson et al. (1952) conducted the most thorough analysis of breeding biology and behavior of *Corynorhinus townsendii* to date. Except where otherwise noted, the information on breeding that follows is summarized from their work.

**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. Once the hibernation period ends and the bats disperse, males are completely dissociated from the reproductive process. Males play no role in rearing young and are rarely present in the roosts of pregnant and lactating females (Kunz and Martin 1982). Thus, care and nurturing of the young falls solely to the female.

Townsend's big-eared bat is seasonally monestrous (Figure 9), and females enter estrous in late summer or early autumn. Mating is most vigorous during this period. Copulation may also take place sporadically through the winter during periodic arousals from torpor. Although coitus primarily occurs in the hibernacula, some females arriving at the hibernacula in late October were already inseminated, suggesting onset of copulation before arrival at hibernation roosts (see discussion below in Breeding behavior). Females store sperm during the hibernation period and do not ovulate until arousing from hibernation in spring. Due to the physiological constraints imposed by hibernation, females suspend normal progression of the reproductive cycle following estrous and mating. Delayed fertilization is one of several reproductive delay strategies employed by bats and other mammals. It is the most commonly described strategy among species of bats that hibernate (Oxberry 1979), and in all likelihood, it is the strategy employed by Townsend’s
big-eared bat. As with other reproductive delays, it is hypothesized to synchronize parturition to periods of optimal food resources and developmental conditions for the young (Racey 1979). Delayed fertilization entails the prolonged storage of sperm in the female reproductive tract following copulation and during the hibernation period. Upon emergence in the spring, ovulation occurs and fertilization, implantation, and gestation then progress normally (Neuweiler 2001). The gestation period varies from 40 to 60 days, and the duration apparently depends on ambient temperature (Kunz and Martin 1982) and levels of precipitation (Grindal et al. 1992). Parturition occurs mid-summer, coinciding with periods of high prey availability. In general, timing of parturition appears 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 volant by 3 weeks of age, but they continue to receive milk for up to 6 weeks following birth.

The most important factors influencing the duration of gestation and the timing of parturition in insectivoros bats relate to the ability of females to allocate energy to the developing fetus or offspring. Females in poor body condition and yearling females generally give birth later than adult females with greater energy reserves. When spring and summer 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 fetal development and offspring growth and development (Racey 1969). Under these conditions, females of other species of bats may forego reproduction and abort or resorb the embryo (Grindal et al. 1992, Lewis 1993); this likely also occurs with Townsend’s big-eared bats. During an unusually cool wet year in the Black Hills, no juvenile Corynorhinus townsendii were captured, and surveys at two maternity colonies indicated either very late parturition (probably early August) or no births during that summer. In contrast, parturition occurred in mid-May the previous year (Tigner and Dowd Stukel 2003).

Breeding behavior

For bats that hibernate, mating generally occurs at hibernacula but may also occur at “swarming sites” or interim roosts after dissolution of maternity colonies but before the onset of hibernation (e.g., Thomas et al. 1979). Swarming sites may be used as hibernacula by some or all of the individuals that aggregate there (Thomas et al. 1979). In general, males mate with multiple females, and multiple males inseminate a female. It is possible, but not known, that select male Corynorhinus townsendii may sire a disproportionate share of offspring, as is the case for other mammals (including bats) with this type of mating system. For example, Watt and Fenton (1995) found evidence of skewed paternity among maternal colonies of the little brown bat (Myotis lucifugus). Although the situation with respect to Townsend’s big-eared bat is unresolved (and, to our knowledge, has not been studied), work on a similar species, the brown long-eared bat (Plecotus auritus), in Europe provided evidence that while males from different colonies typically sired offspring, there was no indication of skewed paternity among offspring (Burland et al. 2001). Because brown long-eared bats are similar to Townsend’s big-eared bats in having limited dispersal and high natal philopatry (Burland et al. 2001), sires from colonies outside the areas in which maternity colonies occur likely serve to minimize inbreeding and to increase genetic diversity (Veith et al. 2004).
Males appear to be largely responsible for initiation of breeding, while females appear to be passive participants in the copulatory process. Pearson et al. (1952) noted pre-copulatory behavior by observing four males and one unmated female in the laboratory. Males approached the pendant female from the front while vocalizing (“making twittering sounds”) and embraced her. For a period of some minutes during the embrace, the male “vigorously rubbed his snout over the face, neck, forearms and ventral surface of the female.” This behavior was thought to involve the enlarged nose glands (Figure 2) and was interpreted to be an attempt to encourage capitulation of the female. The female apparently was unyielding, however, and no description of copulatory behavior was recorded. Pearson et al. (1952) observed one instance of copulation in a cave, and they noted that the pair was oriented “in the usual manner of copulating mammals.”

Fecundity and survivorship

Because of their unique life histories, bats produce relatively few offspring during each reproductive cycle compared to other small mammals. Like many other insectivorous bats, Townsend’s big-eared bat produces a maximum of one young per year. Additionally, females are apt to forego reproduction in some years due to poor body condition, low prey availability, or cool temperatures (Grindal et al. 1992, Lewis 1993, Racey and Entwhistle 2000, Barclay et al. 2004). Because initiating pregnancy upon spring arousal from hibernation requires some minimum level of energy reserves (Kunz et al. 1998), females that emerge from hibernation with very low energy stores may not be capable of the additional energetic requirements of pregnancy and lactation. In addition, females that initiate pregnancy may abort if subsequently faced with cool, wet weather and concomitant reduction in prey availability and increased thermoregulatory costs. For example, Lewis (1993) found a negative correlation with spring temperatures and proportion of non-breeding females in pallid bat colonies, and Grindal et al. (1992) concluded that high levels of precipitation during spring and summer resulted in increased incidence of non-reproductive females in little brown bats and Yuma myotis (Myotis yumanensis). Therefore, the maximum annual reproductive output of one offspring per female for Townsend’s big-eared bat is likely not realized for all females every year. Because conditions in the hibernacula (e.g., temperature, frequency of arousal) influence, in part, body condition in the spring, increased levels of disturbance during the winter may also affect reproductive output.

Bats in general have remarkably long life spans for their size. Paradiso and Greenhall (1967) recorded an age of 16 years 5 months for an individual Corynorhinus townsendii in California, and more recently a new longevity record of greater than 21 years was established (Perkins 1994). Although these data cannot be considered to represent average values for C. townsendii, they do demonstrate the remarkable potential for longevity that appears to be characteristic of bats. Such life spans reflect high survivorship in adults. However, juvenile survivorship appears to be much lower in C. townsendii and other species of bats. The mortality rate of juvenile C. townsendii was estimated to be 38 to 54 percent (Pearson et al. 1952). Survival in subsequent years, however, jumps markedly to about 80 percent (Pearson et al. 1952). Loss of some bats between birth and their first full summer must surely be attributable to a lack of sufficient fat reserves to survive hibernation. However, Pearson et al. (1952) noted relatively few young bats present in hibernacula, which led them to speculate that most juvenile mortality occurred prior to the bats entering hibernation. Whatever the mechanism, the fact remains that juvenile bats experience relatively high rates of mortality while adults appear to have high probability of surviving.

The lack of more recent studies on survivorship in Corynorhinus townsendii and other species of bats may be surprising. However, it is important to recognize that such studies rely primarily on resighting or recapture of banded individuals, the latter of which is often done in hibernacula or maternity roosts and requires handling of substantial numbers of bats (e.g., Mohr 1952, Hitchcock 1965). These activities, common in the mid-1900’s, were largely discontinued by the 1970’s. Concern that the activities of researchers were, in concert with other extrinsic factors, effecting a decline in numbers of cave-dwelling species of bats (Mohr 1953), resolutions were adopted in the early 1970’s that limited the tolerance of such research (Henshaw 1972). In particular, the widespread practice of bat banding was deemed a potential source of added mortality because of the possibility of injuries from bands (e.g., Humphrey and Kunz 1976, Pierson and Fellers 1993) and because banding often occurred at hibernacula. Thus, the practice of bat banding fell out of favor and remains so today (e.g., Baker et al. 2001).

Population demography

Life history parameters

As a group, bats live longer and have lower reproductive output than would be predicted for
mammals of their size (Barclay and Harder 2003). Bats may live several decades, and most give birth only once per year to one or two pups, a life history that contrasts markedly from small terrestrial mammals. Nocturnality and flight are characteristic traits of bats, and these have played important roles in the evolution of life histories of bats (Barclay and Harder 2003), primarily by reducing predation pressure (Speakman 1995).

An important consequence of their low reproductive rate is that bat 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 Corynorhinus townsendii that are relatively sedentary and exhibit a high degree of site fidelity (Kunz and Martin 1982).

Spatial characteristics and genetic concerns

Currently, no studies are available that address the level of genetic diversity within populations of Corynorhinus townsendii. 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 may be separated by patches of unsuitable habitat. Therefore, local populations may exist in relative isolation, and opportunity for immigration into unoccupied habitat may be limited. Consequently, gene flow between populations may be also limited. As shown with other species, it is possible that genetic diversity may be maintained by mixing of individuals from different parts of their range when they aggregate at hibernacula or interim roosts where mating occurs (e.g., Burland et al. 2001). However, C. townsendii appears to be a relatively sedentary species that is not known to engage in long-distance migration to hibernation sites (Kunz and Martin 1982), so it is unclear how extensive such mixing might be for this species. Further research is necessary before conclusions on the degree of genetic isolation among populations of C. townsendii can be drawn.

Life history model

The information presented here detailing the influence of life history parameters on population levels is summarized from matrix models created by Dave McDonald and Takeshi Ise for this conservation assessment. Because of the highly technical nature of the methods, we have summarized the most important results and findings from the models, and we refer the reader to Appendix B for a more technical discussion of the model results. Specifically, we discuss how birth rate, survival rate, and probability of reproduction at various age classes affect population structure. Additionally, we interpret the results of the model in the context of current theories regarding chiropteran life history, which suggest that factors identified by the model as being most influential to population dynamics of Corynorhinus townsendii result in part from their evolutionary history.

Model description

Terms in the model: Three inputs are used to model population dynamics: $P_i$ describes the probability of survival from one age class to the next (i.e., a survival rate); $B_i$ describes the probability that a female will reproduce in the $i^{th}$ age class; $m_i$ describes the number of female offspring produced by the $i^{th}$ female and captures the concept of fertility or fecundity (Table 8). Collectively, these three inputs are termed the vital rates of the model. In addition, because both $P_i$ and $B_i$ effect changes in the number of individuals in younger or older age classes, they are referred to as transitions. The relationship between these terms and the number of individuals in each age class is expressed graphically in the life cycle diagram (Figure 10) and in matrix form (Table 9).

Features and assumptions of the model: The life history model is an age-structured population model, based on Leslie matrices, that examines how various life history attributes combine to influence population dynamics in a closed population, with specific reference to females. That is, the model focuses on the distribution of females among various age classes and how class-specific vital rates drive population dynamics through time. These models are widely applicable to many biological systems and taxa, which has led to their frequent use in conservation biology (Mills et al. 1999).

The model comprises a series of discrete bins (age classes or stages) wherein individuals advance from one age class to the next, and where the probability of advancing (i.e., the probability of surviving from age $i$ to age $i+1$) depends on and varies by class. Similarly, the probability that a female will reproduce, and the number of female offspring she bears will vary among age classes. Thus, the model may be viewed as a system in which individuals flow from birth (youngest age class) to death while producing some number of offspring along the way, and the reproductive output of all age classes replenishes the pool of individuals in the youngest age class. The model is iterated across
Table 8. Parameter values for the component terms \((P_i, m_i, \text{ and } B_i)\) that make up the vital rates in the projection matrix for Townsend’s big-eared bat.

<table>
<thead>
<tr>
<th>Parameter</th>
<th>Numeric value</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>(m)</td>
<td>0.5</td>
<td>Number of female offspring produced by a female</td>
</tr>
<tr>
<td>(B_1)</td>
<td>0.9</td>
<td>Probability of reproduction of Age Class 1</td>
</tr>
<tr>
<td>(B_a)</td>
<td>0.95</td>
<td>Probability of reproduction of Age Class 2 to 5 (adult females)</td>
</tr>
<tr>
<td>(P_{21})</td>
<td>0.576</td>
<td>First-year survival rate</td>
</tr>
<tr>
<td>(P_a)</td>
<td>0.85</td>
<td>Annual survival rate of adults</td>
</tr>
</tbody>
</table>

Figure 10. Age-classified life cycle graph for Townsend’s big-eared bat. The numbered circles (nodes) represent the six age classes. The arrows (arcs) connecting the nodes represent the vital rates – transitions between age classes such as survival \((P_{ji})\) or fertility (the arcs pointing back toward the first node from Nodes 1 through 5). Note that reproduction begins at the end of the first year, and that the reproductive arcs include terms for survival of female parent \((P_i)\) as well as number of female offspring per female \((m_i)\).

Table 9A. Symbolic values.

<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
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<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
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<td>(P_{21}mB_{1})</td>
<td>(P_{32}mB_{a})</td>
<td>(P_{43}mB_{a})</td>
<td>(P_{54}mB_{a})</td>
<td>(P_{65}mB_{a})</td>
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</tr>
<tr>
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<td>(P_{21})</td>
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<td></td>
<td></td>
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<tr>
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<td>(P_{a})</td>
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<td>6</td>
<td>(P_{a})</td>
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Table 9B. Numeric values.

<table>
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<th>4</th>
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<th>6</th>
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<td>2</td>
<td>0.576</td>
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<tr>
<td>3</td>
<td></td>
<td>0.85</td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td>0.85</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
<td></td>
<td></td>
<td>0.85</td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>0.85</td>
<td></td>
</tr>
</tbody>
</table>

Table 9. The input matrix of vital rates, \(A\) (with cells \(a_{ij}\)) corresponding to the Townsend’s big-eared bat life cycle graph (Figure 10). The first row of the matrix contains values associated with reproductive output for a given stage class. Values in the other rows represent the probabilities of an individual moving from one stage to the next.
a number of generations, and the outcome of these iterations is a discrete estimate of population growth ($\lambda$) through time.

It is important to note that these models are designed to assess the effects of changes to intrinsic, rather than extrinsic, factors. For instance, the contribution of a particular age class to increases in population size (i.e., births) will depend both on the probability of surviving to that class and the probability of reproducing in that age class (Figure 10), but not on specific perturbations affecting habitat availability or quality. Nonetheless, if a perturbation (extrinsic factor) is known to affect an intrinsic factor in a specific manner, say, by reducing fertility or survivability of a particular age class, then revised estimates of those intrinsic factors can be incorporated into a revised model. Knowing the relative importance of age-specific life history variables in terms of population dynamics, therefore, permits analysis of which terms are most important for population dynamics.

**Model results and discussion:** The major results from the life history model are that both survival and fertility are key factors to population viability of *Corynorhinus townsendii*, but survival appears to be more important to overall population dynamics. In particular, females in the second age class are expected to be key components of populations of *C. townsendii*. These females, having successfully transitioned to Age Class 2 (i.e., survived their first winter), are not only substantially more likely to survive future winters (85 percent versus 58 percent for Age Class 1 individuals), but they also have the greatest reproductive value (Table 10). Therefore, extrinsic factors that lower or restrict recruitment of females into Age Class 2 will have disproportionate effects on population dynamics. Moreover, in the absence of density-dependent survival or reproduction, a decline in first-year survival (i.e., lower recruitment of second-year females) is likely to generate a cascading effect that may have serious consequences for long-term population stability. That is, reduced recruitment of Age Class 2 females may lead to a slight reduction in the number of juveniles, which in turn could lower the pool of individuals that may be recruited into the second age class.

Results of the model presented thus far are derived from a deterministic model, in which life history parameters were not permitted to vary. This restriction was necessary to tease apart important transitions, and it highlighted the importance of survival of Age Class 2 females relative to other age classes. An alternative use of the model is to gauge the effects of stochastic variation in these values by allowing life history variables to fluctuate.

Based on outcomes from the stochastic model (Table 11), three important results are discernable: 1) variation in survival rates had a somewhat greater effect on $\lambda$ than did variation in fertilities; 2) negative population effects were exacerbated by slight fluctuations in the magnitude of the variation, and; 3) population dynamics were negatively affected as variation in values for life history variables increased, even though average vital rates remained the same as under the deterministic model. Cumulatively, these results suggest that *Corynorhinus townsendii* are vulnerable both to stochastic fluctuations in reproduction rate and to variations in survival.

The matrix model points to adult survival as the primary source of stability in populations of Townsend’s big-eared bat, but it tells us little about why this should be the case. To understand the reasons why, and to evaluate whether the results of this model are consistent with life history theory in general, we now review some current theory regarding the evolution of bat life histories.

**Table 10.** Reproductive values for female Townsend’s big-eared bats. Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The relatively low peak reproductive value is highlighted.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Description</th>
<th>Reproductive values</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Female newborns ($F_i = 0.2592$)</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>Adult females ($F_i = 0.40375$)</td>
<td><strong>1.29</strong></td>
</tr>
<tr>
<td>3</td>
<td>“ ”</td>
<td>1.04</td>
</tr>
<tr>
<td>4</td>
<td>“ ”</td>
<td>0.75</td>
</tr>
<tr>
<td>5</td>
<td>“ ”</td>
<td>0.40</td>
</tr>
<tr>
<td>6</td>
<td>Maximum Age Class</td>
<td>0.00</td>
</tr>
</tbody>
</table>
From a life-history standpoint, temperate-zone insectivorous bats are characterized by a combination of relatively long life span and low annual reproductive output. This condition departs radically from the life histories of other small mammals, which generally reproduce quickly and die young (Findley 1993). A recent analysis of the life history of bats identified reduction in extrinsic mortality (spurred by the development of flight) as a key factor in the evolution of longevity in bats, and proposed that increased longevity in turn allowed low annual reproductive output (Barclay and Harder 2003). Thus, low extrinsic mortality and low fecundity have become tightly coupled during the evolution of bats. This coupling underscores the importance of survival relative to fertility and is consonant with the results of the matrix model. This further highlights the need to minimize or eliminate extrinsic sources of mortality to conserve populations of *Corynorhinus townsendii* from peril.

Another consequence of the unique life histories of bats, and one that follows from the link between longevity and low reproductive output, is that females may increase their fitness by foregoing reproduction during “bad” years. Because *Corynorhinus townsendii* cannot produce more than one offspring per year per female, the ability to offset lost reproductive output from “bad” years with more than one offspring per female during “good” years does not exist. Hence, when levels of extrinsic mortality exceed those under which the life histories of bats evolved, population declines are almost certainly the inevitable outcome.

Community ecology

**Figure 11** presents an envirogram for Townsend’s big-eared bat. An envirogram provides a graphical representation of the web of factors that influence the ability of a species to survive and reproduce, but it does not represent the relative strength or importance of the factors. Much of the community ecology of *Corynorhinus townsendii* discussed in the following sections is captured graphically in this envirogram, which is divided into three basic types of elements influencing bat ecology: resources, malentities, and predators (Andrewartha and Birch 1984).

Townsend’s big-eared bat (as well as other species of bats) fills important ecological roles by providing unique and important ecosystem services (Ducummon 2000, Agosta 2002). Insectivorous bats, such as *Corynorhinus townsendii*, are the only night-time consumers of flying insects. Because many species of insect pests are nocturnally active (Wilson 2004), they are available to bats as prey. Bats may therefore represent effective and essentially free sources of biological control, particularly when pest populations peak. During outbreaks, bats may shift diet to the relatively more abundant pest species (Wilson 2004). Therefore, they may mitigate pest-related damage and loss, and provide concomitant economic benefits. Colonies of Mexican free-tailed bats (*Tadarida brasiliensis*) and big brown bats (*Eptesicus fuscus*) regularly consume vast quantities of insects, many of which are responsible for substantial economic damage to agricultural crops.

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**Table 11.** Summary of three variants of a stochastic projection for Townsend’s big-eared bats.

<table>
<thead>
<tr>
<th>Input factors:</th>
<th>Variant 1</th>
<th>Variant 2</th>
<th>Variant 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Affected cells</td>
<td>$P_i$</td>
<td>$P_i$</td>
<td>$P_i$</td>
</tr>
<tr>
<td>S.D. of random normal distribution</td>
<td>1/4</td>
<td>1/4</td>
<td>1/3.5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Output values:</th>
<th></th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Deterministic $\lambda$</td>
<td>1.00010</td>
<td>1.00010</td>
<td>1.00010</td>
</tr>
<tr>
<td># Extinctions / 100 trials</td>
<td>20</td>
<td>66</td>
<td>82</td>
</tr>
<tr>
<td>Mean extinction time</td>
<td>1,657.4</td>
<td>1,344.2</td>
<td>1,135.3</td>
</tr>
<tr>
<td># Declines / # survived pop</td>
<td>73/80</td>
<td>31/34</td>
<td>18/18</td>
</tr>
<tr>
<td>Mean ending population size</td>
<td>8,254.5</td>
<td>2,166.2</td>
<td>365.0</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>41,190.3</td>
<td>5,895.7</td>
<td>865.2</td>
</tr>
<tr>
<td>Median ending population size</td>
<td>299.16</td>
<td>134.11</td>
<td>49.93</td>
</tr>
<tr>
<td>Log $\lambda$</td>
<td>-0.00269</td>
<td>-0.00548</td>
<td>-0.00766</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>0.9973</td>
<td>0.9945</td>
<td>0.9924</td>
</tr>
<tr>
<td>% reduction in $\lambda$</td>
<td>0.279</td>
<td>0.557</td>
<td>0.773</td>
</tr>
</tbody>
</table>

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Community ecology

**Figure 11** presents an envirogram for Townsend’s big-eared bat. An envirogram provides a graphical representation of the web of factors that influence the ability of a species to survive and reproduce, but it does not represent the relative strength or importance of the factors. Much of the community ecology of *Corynorhinus townsendii* discussed in the following sections is captured graphically in this envirogram, which is divided into three basic types of elements influencing bat ecology: resources, malentities, and predators (Andrewartha and Birch 1984).

Townsend’s big-eared bat (as well as other species of bats) fills important ecological roles by providing unique and important ecosystem services (Ducummon 2000, Agosta 2002). Insectivorous bats, such as *Corynorhinus townsendii*, are the only night-time consumers of flying insects. Because many species of insect pests are nocturnally active (Wilson 2004), they are available to bats as prey. Bats may therefore represent effective and essentially free sources of biological control, particularly when pest populations peak. During outbreaks, bats may shift diet to the relatively more abundant pest species (Wilson 2004). Therefore, they may mitigate pest-related damage and loss, and provide concomitant economic benefits. Colonies of Mexican free-tailed bats (*Tadarida brasiliensis*) and big brown bats (*Eptesicus fuscus*) regularly consume vast quantities of insects, many of which are responsible for substantial economic damage to agricultural crops.
Figure 11. Envirogram for Townsend’s big-eared bat (after Andrewartha and Birch 1984).
(Whitaker 1995, McCracken 1996) and which may develop resistance to widely-used chemical controls (Ducumnon 2000). Similarly, bats that live in forests consume untold quantities of moths and beetles, some of which are considered pest species that damage or kill large numbers of trees during outbreaks (e.g., Wilson 2004). In addition to capturing flying prey, Townsend’s big-eared bats can also glean insects from foliage and are therefore not limited to aerially-active individuals.

Insectivorous bats also are influential in transferring soil nutrients, notably nitrogen, from foraging areas to roosting areas, via their feces (Pierson 1998). Thus, the ecosystem and community ecology roles played by bats likely provide benefits that exceed any of the negatives usually attributed to bats. Effectively conveying this message to the public, which often holds a generally negative perception of bats, is likely to pay benefits in the form of increased support for conservation efforts. See our discussion below under Tools and practices for a more detailed discussion of education goals and strategies.

Predators and competitors

Community ecology of bats is greatly influenced by their life histories, which are typically characteristic of K-selected species: low reproductive rates, long life span, and low extrinsic mortality (Findley 1993). Bats’ nocturnal activity, aerial foraging, and secretive roosting habits have all served to reduce predation pressure, but they do not completely escape predation. Townsend’s big-eared bat may be more susceptible to predation than some other species of bats owing to its colonial and visible roosting habits. Predators such as snakes, raccoons, and small mammalian carnivores take bats opportunistically (Barbour and Davis 1969, Fenton et al. 1994) although specific reports of predation are scant, reports of predation on Corynorhinus 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 in California. 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, remains largely unknown, perhaps owing to the difficulty in witnessing such events.

North-temperate bat communities appear to be saturated (Findley 1993), suggesting that competition may be 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). Although patterns in the structure of local bat assemblages often are suggestive of resource partitioning (e.g., Aldridge and Rautenbach 1987, Crome and Richards 1988), there is as yet little direct evidence of competition between species.

Although Townsend’s big-eared bat is known to share roost sites with other species (see below) and visit the same watering holes that are used by other species of bats (e.g., Adams et al. 2003), no studies have attempted to directly assess competitive interactions between Townsend’s big-eared bat and other species of bats. However, several attempts to demonstrate competition between morphologically similar species of insectivorous bats have been made by focusing on the degree of niche overlap between similar sympatric species. For example, morphologically similar species of Myotis showed greater dietary overlap in allopatry than in sympatry (Husar 1976), and morphologically similar sympatric species of Myotis segregated foraging space and prey items (Arlettaz 1999, Siemers and Swift 2006). These lines of evidence, while not conclusively demonstrating competition, nonetheless illustrate that for bats exploiting essentially the same prey resource in similar ways, the means to avoid direct competition exist (Siemers and Swift 2006). In addition, different species of bats often 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 resources. For example, the silver-haired bat (Lasionycteris noctivagans) alters its activity period when sympatric with ecologically similar species such as Eastern red bat (Lasiurus borealis), the hoary bat, and the big brown bat (reviewed in Kunz 1982). However, because competition is difficult to demonstrate, even between closely related sympatric species (Arlettaz 1999), questions regarding the extent to which competition shapes the ecology of Townsend’s big-eared bat remain open.
Parasites and disease

In general, a number of external parasites complete all or part of their life cycles on bats, and two species of fleas (*Nycteridopsylla vanouverensis* and *Myodopsylla palposa*) have been identified from Townsend’s big-eared bats (Haas et al. 1983). Although the effects of parasites on bats are generally unknown, Lewis (1995) hypothesized that reduction of parasite loads should increase fitness and may partially explain roost-switching behavior.

As with other mammals, *Corynorhinus townsendii* can be a vector for the rabies virus, but no estimates of the prevalence of rabies in Townsend’s big-eared bat exist. In general, the incidence of rabies in wild populations of bats appears to be exceedingly low (see below), and it poses minimal threat to humans (Constantine 1979, Constantine et al. 1979) and no threat to the persistence of the species. Despite the facts of the situation, the perception of bats as deadly vectors of rabies has greatly harmed their image and resulted in public desire to exterminate bats. Bat Conservation International (BCI), provides a concise account of the bat-rabies connection on its website (http://www.batcon.org/), from which some of the following information was derived.

Historically, most rabies transmission to humans occurred in domestic animals (e.g., cats and dogs), but following widespread pet vaccination programs, wild animals now represent the bulk of animal rabies cases. Wild animals accounted for about 93 percent of animal rabies cases reported to the Centers for Disease Control in 2001, of which 37.2 percent were raccoons, 30.7 percent skunks, 17.2 percent bats, 5.9 percent foxes, and 0.7 percent other wild animals (Krebs et al 2001), but neither the total number and type of animals turned in nor the methods for their collection were reported. The apparently large proportion of bats in this list may be partially due to a recent increase in the prevalence of bats being turned in to disease professionals (Wadsworth Center 2000). Some state-level reports suggest that bats turned into health departments have a lower incidence of rabies infection (often less than 10 percent of cases), suggesting that the prevalence among the entire wild population is smaller still, perhaps on order of 0.5 to 1.0 percent (e.g., Caire 1998, Wadsworth Center 2000, Willkerson 2001, South Dakota Bat Working Group 2004) or lower (Constantine 1979).

Further, bats rarely transmit fatal rabies infections to humans, as evidenced by the fact that rabies viruses attributed to bats that commonly live in buildings have only been associated with eight human fatalities in all of U.S. history, and the most common bat in Region 2, the little brown bat, has never been documented transferring rabies to humans. Only a bite from an infected bat that breaks the skin can transmit the rabies virus; the virus has not been isolated from bat blood, urine, or feces, and there is no evidence of air-borne transmission in buildings. Thus, the most likely way for someone to get rabies from a bat is to disturb an evidently sick bat to the point that it inflicts a severe bite, and even then, only a small portion of noticeably sick bats actually have rabies. Since normal, healthy bats will usually not allow themselves to be contacted by humans (unless they are in a state of torpor during roosting), virtually all risk of exposure can be eliminated by not handling live bats that allow such contact. If frequent interaction with live bats is a regular occurrence, a highly effective and painless vaccine is available that further reduces risk of transmission. Primary care doctors or public health officials can usually order and administer this vaccine.

More recently, West Nile virus has been confirmed in bats from a small number of cases in the United States (Gould and Fikrig 2004). However, the degree to which bats are exposed to this virus and the potential for population-level effects are currently unknown. Moreover, bats are likely beneficial in controlling West Nile virus through the consumption of mosquitoes, which are the primary vectors for the disease.

Symbiotic and mutualistic interactions

No symbiotic or mutualistic relationships are known between *Corynorhinus townsendii* and other species of plant or animal. Although *C. townsendii* is known to share roosts with other species of bats, no hypotheses regarding mutual benefits have been proposed. When other species are found roosting in the same cave or mine as *C. townsendii*, they are not intermixed, but instead occupy discrete places within the roost.

Species of bats known to occupy roosts with Townsend’s big-eared bats include (in no particular order): pallid bat, Rafinesque’s big-eared bat (*Corynorhinus rafinesquii*), Mexican big-eared bat (*C. mexicanus*), big brown bat, Allen’s big-eared bat (*Idionycteris phyllotis*), California leaf-nosed bat (*Macrotus californicus*), southwestern myotis (*Myotis auricus*), California myotis (*M. californicus*), western small-footed myotis (*M. ciliolabrum*), western long-eared myotis, little brown bat (*M. lucifugus*), Indiana bat (*M. sodalis*), fringe myotis (*M. thysanodes*), cave myotis (*M. velifer*), long-legged myotis (*M. volans*), Yuma myotis, western pipistrelle (*Pipistrellus volans*), Mexican big-eared bat (*M. sodalis*), big brown bat, Allen’s big-eared bat (*M. ciliolabrum*), Myotis (e.g., *M. lucifugus* and *M. thysanodes*), big brown bat, Allen’s big-eared bat (*M. ciliolabrum*), and *M. velifer*).
hesperus), eastern pipistrelle (P. subflavus), and Mexican free-tailed bat (Jagnow 1988, Pierson et al. 1999 and references therein, López-González and Torres-Morales 2004).

**Conservation and Management of Townsend's Big-eared Bat in Region 2**

We have divided this chapter into sections on biological conservation status, comprised of extrinsic threats and intrinsic vulnerability, and management. Biological status synthesizes the key parameters noted earlier in this document that define the conservation status of Townsend’s big-eared bat – specifically, abundance and distribution. Following this, sections on intrinsic factors and extrinsic threats highlight elements that affect biological parameters and thus influence the biological status of the species. Intrinsic factors include those things driven primarily by the biology of the species, such as lifespan and reproductive rate, while extrinsic factors are those driven by external forces, such as predation, habitat loss, habitat disturbance, and reduction of prey base. The chapter concludes with a discussion of specific management objectives and the tools and practices that might be used to facilitate the conservation of Townsend’s big-eared bat.

**Biological Conservation Status**

Abundance and abundance trends

Although Corynorhinus townsendii is geographically widespread, it exists in relatively low density throughout its range (Barbour and Davis 1969, Kunz and Martin 1982), likely because of the relative paucity of suitable roosting habitat and the resulting patchy distribution this creates. Townsend’s big-eared bat is a colonial species and forms aggregations ranging from one to several hundred individuals (Table 6). The size of any particular colony apparently depends on the type of colony and the time of year. Hibernation colonies may range from a few dozen individuals to over 1000 bats (Ellison et al. 2003b). Maternity colonies are generally smaller, usually consisting of a few dozen individuals, but sometimes reaching a few hundred. Bachelor colonies are much smaller, typically consisting of only a few individuals. Relative to maternity or bachelor colonies, hibernation colonies appear to exhibit considerable temporal variation in size during the cold season, ranging from a few individuals to many hundreds at the same site. Variation in size of hibernating colonies may reflect movement of individuals among several hibernation roosts, with individuals arriving at and departing from roosts throughout the cold season. Hibernation colonies appear to remain most stable during the coldest months.

Pierson et al. (1999) reviewed the status of Corynorhinus townsendii throughout its western range, and compiled information on population numbers and trends for individual states. Below we summarize this information for the states within Region 2, and augment the information with more recent data where appropriate.

**Colorado**: Most of the information for Colorado comes from work conducted after 1990. Siemers (2002) conducted a survey that documented 11 maternity roosts in the state, six in caves and five in mines. The largest of these colonies, about 150 bats, was located in a mine. Each of the other sites held small numbers (1 to 8) of bats. Of the 30 hibernacula known from Colorado, only four were known before 1990. Most contained only a few bats, but one roost held over 200 bats. Recent surveys resulted in documented use of 12 caves (eight of which were previously unknown as roosts) by 33 Townsend’s big-eared bats.

**Kansas**: Information on population status of Corynorhinus townsendii in Kansas was unavailable.

**Nebraska**: Corynorhinus townsendii may not be a resident species in Nebraska, as the only record of occurrence is a single male found roosting on a screen door in 1972.

**South Dakota**: Most work in South Dakota has focused on the Black Hills where three maternity colonies (two with 50 individuals, one with 35 individuals) are known. More recently, Tigner and Dowd Stukel (2003) reported two hibernation colonies in Jewel Cave National Monument that collectively contained approximately 1200 Corynorhinus townsendii. There appears to be a general decrease in C. townsendii roosting in Jewel Cave since the mid 1900’s, with the greatest abundance reported as 3,750 in 1959 and a population low of 593 in 1997, which has increased to between 800 and 1200 in recent years (Ellison et al. 2003b).

**Wyoming**: There is little information available on colony size or status prior to 1994. At least three maternity colonies have been identified: one in an abandoned mine and two in caves, harboring 46, 50+, and 200+ individuals respectively, with an additional cave colony reported by Keinath (2005). Surveys at 59 caves and 17 mines conducted in 1994...
resulted in the identification of 12 occupied sites, most containing one to three bats. At this time, only two hibernacula have been found, each containing fewer than four individuals.

Since the early 1970’s, bat researchers have expressed concern about apparent declines in numbers of cave-dwelling species of bats (Henshaw 1972), and *Corynorhinus townsendii* appears not to have been immune to the forces driving these declines. Some reports indicate that western populations of *C. townsendii* have declined markedly since the middle of the 20th century (Perkins and Levesque 1987, Pierson and Rainey 1998, Pierson et al. 1999). However, trends in abundance are difficult to assess in the absence of data on abundance through time, and it is important here to note that long-term monitoring data for Townsend’s big-eared bats (and for most other species of bats) are generally lacking and patchy at best. For example, Ellison et al. (2003b) compiled observations on *C. townsendii* at summer and winter roosts from a wide variety of sources (e.g., federal, state and local reports, Natural Heritage Programs, theses and dissertations, and published articles). Of the counts of *C. townsendii* at 615 colonies that they compiled, only 21 had time series that allowed analysis of trends (n ≥ 4 distinct years). Of these 21, no trend was detected at 17 colonies. Two hibernacula (including Jewel Cave, SD) and one summer colony had statistically significant declines, while one hibernaculum (Middle Butte Cave, ID) showed a significant increase.

Another difficulty in assessing trends comes from variability in data sets. For example, even for the small proportion of colonies available for analysis by Ellison et al. (2003b), variability of numbers recorded across years at some sites varied greatly (see Appendix 6 in Ellison et al. 2003b), leading to reduced statistical power to detect trends. A cursory look at the data from Ellison et al. (2003b) suggests that significant downward trends might have been detected at three additional colonies if data from a single season’s survey were removed from the data set. This variability in numbers may be attributable to methodological differences among studies and/or years, differences in survey timing, or differences in year-to-year productivity and survival. Alternatively, differences may result in part from roost-switching behavior by Townsend’s big-eared bats that may have coincided with survey events, leading to the appearance of low abundance in certain years. We take up this matter in greater detail below.

For Townsend’s big-eared bat, the primary cause for declines has generally been attributed to disturbance by humans at roost sites and uninformed closure of abandoned mines (Barbour and Davis 1969, Pierson et al. 1999, Lacki 2000). Although many species of bats that roost in caves also roost in other structures in various parts of their range, Townsend’s big-eared bat relies on caves and cave analogs for shelter. Thus, the loss of cavernicolous roosting habitat through disturbance and destruction has likely impacted *Corynorhinus townsendii* to a greater degree than species with more flexible roosting habits.

As noted above, the best available evidence suggests long-term declines in numbers of *Corynorhinus townsendii* at historic sites, with blame often assigned to a reduction of suitable roosting habitat through disturbance and destruction. Undoubtedly, increased levels of human intrusion have affected traditional roosting sites in many areas. These actions are well known to lead to roost abandonment by Townsend’s big-eared bat, and abandonment may lead to reductions in numbers if it results in lowered reproductive success and/or reduced overwinter survival (e.g., Humphrey and Kunz 1976). Thus, even without considering direct mortality of bats because of intrusion, there is a plausible nexus between roost disturbance and reduced numbers of bats.

The nexus between roost disturbance and reduced populations relies in part on the assumption that roosts are a limiting factor for Townsend’s big-eared bat. That is, bats that have been disturbed and abandon roosts may have few alternative sites to which they can go, and these alternative sites may not meet the needs of the bats during a particular life stage. However, the assumption that roosts are limited belies the fact there has been an increase in available roosts relative to pre-settlement times throughout the West. The abandonment of subterranean hard-rock mines over the past century has provided ample additional roosting opportunities, and it is clear that Townsend’s big-eared bats readily use these structures. Although recent mine closures throughout the West have removed some of these roosting opportunities (and in some cases entombed bats within), there remain many thousands of abandoned mines that did not exist a century ago. Thus, that the abundance of this species appears to have declined even while roosting opportunities have increased presents a paradox for which there are not yet satisfactory answers. Any number of possible
explanations, ranging from the simple to the complex, might explain the paradox. Here, we focus on the two principle components of the paradox: that abundance of *Corynorhinus townsendii* has decreased, and that roosting opportunities for Townsend’s big-eared bat have increased.

The assumption that the abundance of Townsend’s big-eared bat has declined throughout much of its western range – one that, given its prominence in the published literature, we have cited throughout this document – is generally based on comparisons of results of recent surveys conducted at historical sites with those of historical surveys. These studies often report reduced numbers, and sometimes a reduction in historical habitat (see Pierson et al. 1999 for overview). However, given that Townsend’s big-eared bat appears to switch roosts more often than previously assumed (Sherwin et al. 2003), we cannot dismiss the possibility that recent surveys have unintentionally missed some bats that possibly were in alternate (but perhaps unknown) roosts. Whether this has happened and whether, if it has, it can account for the reductions in numbers reported are questions for which we have no definitive answers. Still, these data represent the best estimates currently available. We therefore must assume that they reflect recent trends in abundance, and conclude that declines in *Corynorhinus townsendii* less than or equal to those reported in the literature likely reflect reality.

What, then, are we to make of the fact that roosting habitat has increased during the same period that population declines are reported to have occurred? An increase in roosting habitat should, according to ecological theory, lead to an increase in numbers of those animals that rely on the habitat. Yet, our best evidence indicates that the opposite has occurred. One possible explanation is that although use of abandoned mines by *Corynorhinus townsendii* is common, these roosts may provide poor roosting conditions. For instance, mines used by a local population may be only marginally suitable for rearing offspring or for hibernation, with the result being a long-term decline in population numbers. As well, if bats using mines are exposed to sub-lethal concentrations of environmental toxins that compromise reproductive ability of adults and/or survival of young (reviewed below under Pesticides and Environmental Toxins), then the bats may experience slow or negative long-term population growth. In either case, immigration from other areas could help to bolster populations, but because of its sedentary nature, *C. townsendii* may not readily immigrate into new locales. Moreover, if slow or negative population growth is characteristic of local populations within a region, then an excess of individuals that could drive immigration is not likely to exist. Here, then, is a possible (albeit speculative and untested) scenario by which an increase in roosting habitat has not led to increased numbers of Townsend’s big-eared bats.

An alternative (and equally speculative) explanation for the paradox rests on the idea that abundance of this species is now roughly the same as it has always been, but that the bats are now more dispersed on the landscape leading to a lower overall density of bats. Altenbach and Sherwin (2002) speculated that an increase in the quantity of roosts (i.e., abandoned mines) may have served to distribute bats more evenly in space, but it might not necessarily have resulted in increased numbers of bats. This may seem an unlikely scenario, yet there is no denying that abandoned mines have increased the number of roosting opportunities (relative to pre-European settlement) for Townsend’s big-eared bat, even while populations appear to be on the decline. Altenbach and Sherwin (2002) proposed limitations in availability of energy as a possible mechanism by which this scenario might be realized, but other mechanisms are also possible (e.g., see our discussion above). Moreover, the idea that *Corynorhinus townsendii* might disperse into new habitat and yet not realize increased numbers was hypothesized earlier. Humphrey and Kunz (1976) previously suggested that *C. townsendii* is a “capable colonizer,” but because of inherent life-history limitations (i.e., below average natality and above average pre-weaning mortality relative to other species of colonial bats in their study area), they may be unable to realize the large populations seen in other species of colonial bats. Thus, although we can be relatively certain that *C. townsendii* are now more dispersed than before hard-rock mining began in the West, they may indeed exist at lower densities than they did previously. If so, survey results that suggest reduced numbers of bats may reflect real reductions at a particular site or sites, but they may not necessarily reflect actual population declines at broader geographic scales.

We must stress that the preceding discussion is highly speculative. Although Townsend’s big-eared bat is almost certainly more dispersed now than it was historically (e.g., Sherwin et al. 2000a), it remains unclear whether such a re-distribution of the population has had negative, neutral, or positive consequences for populations at various geographic scales. If greater numbers of Townsend’s big-eared bat now exist in more locations, it is likely that surveys would have reflected an increase. Thus, we conclude that numbers of *Corynorhinus townsendii* have, for currently unknown reasons, experienced declines throughout the West. Any
actions, therefore, that safeguard known roosts, maintain and enhance roosting opportunities at suspected roosts (e.g., through pre-closure screening and gating of mines), and bolster the quality and quantity of other habitat components (e.g., foraging and drinking areas) are likely to reap conservation benefits.

Distribution trends

Spatial distribution

Townsend’s big-eared bat is distributed widely across western North America. However, local distribution is bounded by the presence of caves and similar structures, most of which are the result of specific geological conditions and processes, and which are not distributed evenly across the landscape. As the distribution of these structures on the landscape is patchy, so too is the distribution of Corynorhinus townsendii. Relatively recent anthropogenic activities have created new roosting opportunities, but most of these new roosts apparently were created within the existing range of C. townsendii (Altenbach and Sherwin 2002).

Within areas containing roosting habitat, there is evidence of sexual segregation by Corynorhinus townsendii during the warm season. In the Black Hills, reproductive females were more abundant at lower elevations than at higher ones. This may reflect the more restrictive thermoregulatory needs of females (Cryan et al. 2000), and it may reflect the distribution of roosts with suitable (i.e., warmer) microclimates for reproductive females. In northwestern Wyoming, males were found roosting singly in less consistently warm environments than the maternity colonies of females (Keinath 2005). In contrast to maternity colonies, hibernacula (usually caves) host both sexes and can be located at higher elevations or in areas that get cold in the winter, presumably to exploit the consistently cool temperatures found in those features. As with summer distributions, the winter distribution of C. townsendii will be determined not only by the location of roosts, but also by the subset of those roosts that have suitable environmental conditions, in this case generally humid areas with temperatures that are consistently just above freezing throughout the hibernation period.

Given the general lack of data on the historic distribution of Corynorhinus townsendii, current distribution trends are difficult to assess. At the broadest scale, there is no evidence of significant range expansion or contraction for C. townsendii. Documented changes in local populations have been quite variable (Altenbach and Sherwin 2002) and do not appear to suggest a consistent range-wide trend. It is possible that local or regional distributions of C. townsendii have become more evenly spread across the landscape over the past decade (Altenbach and Sherwin 2002), but it is difficult to construct a clear or consistent picture of such distribution trends. For instance, the absence of C. townsendii from some previously occupied sites (Perkins and Levesque 1987, Pierson and Rainey 1998, Pierson et al. 1999) might suggest a local decrease in distribution (and is often interpreted as a concomitant decrease in numbers of bats), but the species also appears to be present at some formerly unoccupied sites (O’Shea and Vaughan 1999).

Such conflicting evidence raises more questions than it answers. How have changes in distribution affected population stability and viability at local and regional scales? How are managers and biologists to interpret changes in local or regional distributions? What is the appropriate scale at which to assess these changes, and what are the management implications of distributional changes? These questions are of critical importance to management of Townsend’s big-eared bats and the resources on which they depend. Therefore, the remainder of this section draws on themes developed in the previous sections in an attempt to address these questions and to provide a framework within which to base management and conservation decisions. We begin with a discussion of how distributional changes may influence populations of Corynorhinus townsendii.

As discussed above, additional roosting opportunities for this species have been created for more than a century through the opening and subsequent abandonment of underground mines. Because Corynorhinus townsendii readily use abandoned mines as roosting habitat, the increase in the number of abandoned underground mines may have led to a concomitant expansion in the local or regional distribution of the species. The implications of such changes on populations depend on the extent to which populations are limited by roosting opportunities. Altenbach and Sherwin (2002) proposed three related, but not mutually exclusive, hypotheses to explain how populations may have responded to increased roosting opportunities:

1. The Displacement (Refugia) Hypothesis. It is clear that human disturbance can cause bats, and Corynorhinus townsendii in particular, to abandon caves (see Threats section) although there are a few examples where moderate disturbance has not led to
abandonment (e.g., Sherwin et al. 2000a). Because *C. townsendii* historically roosted in caves, but now regularly roosts in mines as well, it is commonly assumed that mines represent places of asylum into which *C. townsendii* and other cave-dwelling species have been forced by human disturbance at caves. Anecdotal support for this hypothesis comes from cases such as the decline of a cave-based maternity colony of fringed myotis from over 500 females in 1990 to none in 2001, and the coincident increase in the use of a nearby abandoned mine by the colony. Human visitation at the cave during this period increased noticeably and may have been a causative factor. Even given such local shifts, it is not clear that this fully explains patterns of distribution or roost selection at larger scales. It is difficult to extrapolate across scales because such disturbance is not equally expressed throughout the range (e.g., accessibility to caves varies) and availability of caves (particularly those suitable for roosts) varies substantially from location to location.

2. **The Roost-Limited (Range Expansion) Hypothesis.** This hypothesis rests on the assumption that the number of roosts limits distribution and abundance of cave-dwelling species. Since *Corynorhinus townsendii* do not occur where suitable cavernicolous roosting habitat is unavailable, it seems clear that roost availability limits distribution, but the correlation with abundance is more tenuous. If the assumption is valid, then the addition of roosting opportunities in abandoned mines should result in increased population size. However, although a more even distribution of *C. townsendii* and other species has likely resulted from the creation of mines, no discernable trend toward increased abundance at any spatial scale has been documented. As well, roost size and colony size do not appear to be correlated. Assuming that larger roosts provide a greater number of roosting opportunities, this lack of correlation suggests that, in addition to roost limitations, other factors may constrain population size in *C. townsendii*.

3. **The Spilled Milk Hypothesis.** Although the previous two hypotheses have been previously proposed in one form or another, this hypothesis is novel and attempts to disentangle the relationship between distribution patterns and population size. It assumes that the presence of roosts regulates distribution patterns, but that some other (non-density dependent) intrinsic factor constrains population growth (e.g., availability of energy). The analogy is drawn between the volume of milk that exists within a cup and after it is spilled from the cup, where the cup represents roosts, and the milk represents colonies of bats. The volume of milk is constrained by the capacity of the cup. Once spilled, the milk will be more dispersed but the volume does not change. Hence, the addition of roosts on the landscape may serve to more evenly distribute bats (i.e., to “spill” bats across the landscape), but if constraints on population growth other than availability of roosts (e.g., availability of energy) exist, then populations would not necessarily increase in size.

This last hypothesis appears to best explain the observed patterns of distribution and abundance of *Corynorhinus townsendii* in the West. For instance, colonies in mines tend to be smaller and more evenly distributed than those in caves, and size of colonies in mines tends to decrease as distance from portions of range with caves increases (Sherwin et al. 2000a). Thus, although the geographic range of *C. townsendii* has remained relatively static, its local distribution has responded to changing local conditions by becoming more dispersed, without necessarily resulting in increased abundance.

Although hypotheses such as these tend to focus on the theoretical underpinnings of biogeography, there are important management implications associated with each. Effective management of *Corynorhinus townsendii* in Region 2 depends on the scale at which decisions regarding protection of the species and its habitat are made, and those decisions are likely to be site and time specific. For example, in the case of fringed myotis cited above, one might ask whether disturbance leading to displacement had a negative, positive, or neutral effect on the colony. If the disturbance led to a decline in abundance, then the species will have been negatively impacted irrespective of the scale considered. However, if we assume (or know) that numbers remained about the same, the answer will depend on scale. At the regional level, the fact that the same number of bats persists post-disturbance in the same area may lead us to answer that the disturbance was neutral. Locally, however, re-location may involve changes in surface
ownership, management units, or other matters of practical concern, all of which are likely to influence management direction. Even if a displaced colony does not jump geopolitical boundaries, management of a colony in a cave entails different actions and considerations than management of the same colony in a mine (reviewed below), and these things in turn may depend on the scale at which management decisions are made. There are no easy answers, and management approaches must effectively address the issues at the several spatial scales at which bats must be considered. Managers and biologists must determine what events constitute negative impacts and how to maximize long-term stability of populations at multiple scales.

As a final point, the above hypotheses are germane because they lead to fundamentally different conclusions about how changes in distribution affect populations of *Corynorhinus townsendii*. For example, one important implication of the Spilled Milk Hypothesis is that the recent increase in rates of mine closure may profoundly affect population size at multiple spatial scales because, given that the milk is now spilled onto the table, “if the milk is then wiped [away], the total volume of milk [is] reduced” (Altenbach and Sherwin 2002). That is, if populations are now spread thinner, then closure or destruction of roosts used locally by smaller, more dispersed colonies may lead to an overall reduction in abundance at the regional level.

**Temporal distribution**

**Roosts:** Given a roost known to hold *Corynorhinus townsendii*, how likely is it that the bats will be present when the roost is surveyed? Given an unknown (i.e., potential) roost, how many surveys will be required to be confident that no bats use it? These are important questions for management and conservation of Townsend’s big-eared bat because management of roosting habitat depends on knowledge about patterns of roost use, and because much of our information about population size and abundance of *C. townsendii* is derived from surveys conducted at roosts. Therefore, we discuss in this section what is known about how Townsend’s big-eared bats distribute themselves among roosts between seasons, and the degree to which they move among roosts within a season.

The most conspicuous temporal change in distribution of bats occurs during the transitions between warm and cold seasons. As summer wanes, bats begin movements toward wintering grounds. Because *Corynorhinus townsendii* roosts in caves or mines year-round, this seasonal event may or may not entail movement from summering to wintering grounds. That is, roosts used during the summer months are sometimes suitable as hibernacula during the winter. For example, at least one cave in Region 2 is used both as a nursery roost during summer and as a hibernaculum during winter (Tigner and Dowd Stukel 2003). However, roosts used by *C. townsendii* in summer often remain too warm (e.g., because of low elevation) or get too cold (e.g., because of the dimensions of the structure) in winter to be used as hibernacula. Where this occurs, bats move toward more suitable locations for the winter.

Movement to hibernacula begins in late summer or early autumn. Although numbers of bats in a given hibernaculum may be highly variable through autumn, maximum numbers of bats are realized by mid-winter and remain relatively stable through the coldest winter months. As spring approaches, bats begin to arouse more frequently and to move toward summering grounds. In central Oregon, female *Corynorhinus townsendii* leave hibernacula in April but do not move directly to maternity roosts (Dobkin et al. 1995). During this period of up to 2 months, the bats used interim roosts to which they showed little fidelity (Dobkin et al. 1995). Although the precise timing of these events is likely to vary by location, elevation, climate, etc., it is worth noting because it has generally been assumed that *C. townsendii* show high fidelity to particular roosts (Kunz and Martin 1982), and the study from Oregon demonstrates that this assumption may not always hold. This in turn has consequences for survey and management of the species. Until very recently, the degree of roost switching that occurs normally has not been extensively studied.

In one of the most comprehensive studies of inter-and intra-season roosting patterns by *Corynorhinus townsendii* to date, Sherwin et al. (2003) showed that use of caves and mines by Townsend’s big-eared bats appears to be more variable than previously appreciated (see also Sherwin et al. 2000a). Based on repeated surveys at 1392 caves and mines in Nevada and Utah between 1994 and 2001, Sherwin et al. documented a high degree of variability in roost use both within and between seasons, with bats often moving to new roosts several times within a season. In general, bats using mines switched roosts more frequently than those using caves, with hibernacula and bachelor colonies switching roosts more often than maternity colonies. Maternity colonies in mines switched roosts between one and six times (x = 3) during the maternal season, whereas maternity colonies in caves normally used a single cave during the season and across years (Table 12).
Besides human disturbance at roost sites, there are at least two potential explanations for this degree of temporal variability in roost use. The first invokes the empirical relationship between roost fidelity and roost permanence and abundance (Lewis 1995), wherein there appears to be a positive correlation between roost fidelity and highly permanent roosts that occur in low abundance (e.g., caves) and a negative correlation between fidelity and roosts that are more abundant and have low temporal permanence (e.g., mines) (Lewis 1995). A second potential explanation is that roost site conditions may not meet physiological constraints throughout the season. Conditions in the roost can have profound effects on the fitness of bats (e.g., Ransome and McOwat 1994, Thomas 1995). If *Corynorhinus townsendii* are unable to find a single roost that provides the array of conditions necessary to meet physiological needs during various life stages, then they may be forced to seek different roosts during different life stages. If, for example, mines provide a more limited range of environmental conditions (because, for instance, they are shallower, have different airflow regimes, or lack the structural complexity of caves), then this may lead Townsend’s big-eared bats roosting in mines to switch roosts to find more optimal conditions. The same argument could be applied to cave roosts; however, at least within the region studied by Sherwin et al. (2003), colonies displayed greater inter- and intra-seasonal fidelity to caves than mines, suggesting an inherent proclivity by Townsend’s big-eared bat for cave roosts, or a greater diversity of roosting conditions within the structural complexity of caves within and between seasons, or both.

Regardless of the reason, it appears that *Corynorhinus townsendii* exhibits greater temporal roost movement than was previously appreciated. If this observation holds for other portions of the bat’s range, it means that one or two visits to a mine prior to closure may not suffice to establish that Townsend’s big-eared bats do not use the mine. It also means that a single survey conducted at a site once per year to estimate population trends may yield erroneous evidence. We take up this matter in greater detail below in the Tools and practices section.

**Table 12. Patterns of temporal roost use and site fidelity exhibited by Townsend’s big-eared bats in the Great Basin as reflected in effort necessary to eliminate a roost with 90 percent probability. Greater effort was required for groups that switched frequently during a particular season. Use of caves was generally less variable than use of mines. For mines, summer bachelor colonies and small hibernation colonies showed greatest variability in site fidelity and thus required more effort. Large colonies in mines and colonies in caves showed similar patterns of fidelity to particular roosts. Data adapted from Sherwin et al. (2003).**

<table>
<thead>
<tr>
<th>Roost Type</th>
<th>Colony Type</th>
<th>Colony Size</th>
<th>Probability (%) of correctly classifying a site as unused during a season with one visit to the site during the season</th>
<th>Minimum number of surveys needed to identify non-roosts with 90% probability</th>
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<td>Mine</td>
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<td></td>
<td>Bachelor</td>
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<td>Hibernacula</td>
<td>85</td>
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<td>Cave</td>
<td>Summer</td>
<td>70</td>
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*Small colonies were defined as those with 5 or fewer individuals. Large colonies comprised >5 individuals. Use of caves by hibernating colonies was not sensitive to colony size. Greater than 95% of hibernating colonies in caves used a single cave continuously through the cold season. These caves were also used as hibernacula during all years of the study.*

**Foraging:** Most foraging activity by temperate, insectivorous bats occurs soon after sunset, when flying insects are numerous and bats are in need of their first meal since the previous night’s foraging. Townsend’s big-eared bat emerges from its roost and begins foraging later than many other species of bats (Kunz and Martin 1982). Most reports indicate that *Corynorhinus townsendii* begins its nightly foraging about 60 minutes after sunset (Clark et al. 1993, Dobkin et al. 1995). The length of foraging bouts varies, but
initial foraging may last up to 2 hours, followed by a period of rest and digestion at a night roost. Rather than use night roosts, females in the early stages of lactation appear to alternate foraging bouts with return trips to the day roost several times per night to nurse young (e.g., Clark et al. 1993). During late-lactation, females may forage continuously all night long (e.g., Bradley 1996).

As with temporal patterns of roost use, use of foraging areas by Corynorhinus townsendii may also be more variable than has been assumed. Although foraging activity by bats in general at any particular place is likely to fluctuate through time (Hayes 1997), studies of foraging patterns by Townsend’s big-eared bats in Oregon (Dobkin et al. 1995), Nevada (Bradley 1996), and California (Fellers and Pierson 2002) indicate that the bats show high fidelity to particular foraging areas. Although these studies provide important insight into foraging patterns during particular stages of the reproductive cycle, inference to broader temporal patterns is not possible. When a broader period is considered (e.g., over the entire reproductive season), however, patterns emerge that differ from those presumed by fidelity to one or a few foraging sites. For instance, in Kentucky and Oklahoma, reproductive females showed fidelity to particular foraging sites during certain reproductive stages, but they switched locations as the season progressed, with females generally traveling farther to foraging sites and/or increasing the size of foraging areas later in the season (Clark et al. 1993, Adam et al. 1994).

The reason (or reasons) for this shift is poorly understood. One proposed explanation holds that females forage further from roosts to leave nearby foraging sites to newly volant young (e.g., Fellers and Pierson 2002). This is an attractive hypothesis and suggests adaptive behavior that may increase the odds of offspring survival, but the data are insufficient to assess its merits adequately. Another possibility is that during the most energetically demanding stages of reproduction, females cannot afford the energy or the time to fly long distances, and this constraint is reflected in a reduction in distance traveled or size of foraging area. During pregnancy, for instance, females carry the additional weight of the fetus (up to 25 percent of the mother’s mass near term), resulting in increased flight costs and perhaps a tendency to minimize commutes. As well, during the first few weeks of lactation, mothers must return to the roost several times each night to nurse non-volant young (e.g., Clark et al. 1993). Lactating females may therefore forage nearby to minimize energetically expensive flight and time spent commuting that could otherwise be spent nursing or foraging. If so, and all else being equal, females would be expected to be able to increase foraging distance or foraging area during less energetically demanding stages of reproduction (i.e., early pregnancy and late- or post-lactation).

During early pregnancy and late- or post-lactation, females do appear to travel greater distances to foraging sites and/or to increase the size of their foraging areas relative to pregnant and lactating females (Table 7), suggesting that energetic constraints of mothers may be important factors influencing use of particular foraging sites. Although increased travel to foraging sites for late- or post-lactating females may also reflect females bestowing nearby sites to newly volant young, it is difficult to attribute longer commutes during early pregnancy to such behavior. In any case, management efforts to maintain and protect multiple foraging areas in close proximity (e.g., <5 km) to known or probable roosts, as well as foraging sites at distances of up to 10 km (6 miles) from roosts will in all likelihood benefit bats. Such arrangement of foraging habitat would allow reproductive females the flexibility to forage as demands warrant, and allow volant juveniles to exploit nearby foraging sites.

Habitat trends

Roosting habitat

The clearest trends that can be identified in roosting habitat for Corynorhinus townsendii are that mines are being closed at an accelerating rate, often without pre-closure surveys (Altenbach 1998), and that disturbance at caves and abandoned mines over the past 30 years appears to be on the rise (Meier and Garcia 2000). Given the ubiquitous nature of these pressures, and lacking information about trends in cavernicolous roosting habitat for Region 2, it is prudent to assume that trends observed range-wide apply within the Region as well. Mining activity at formerly abandoned sites that have since become used by bats can have effects beyond simple displacement (O’Shea et al. 2000). For example, bats may be exposed to toxic pollutants created by mining operations by drinking from contaminated waters emanating from mines, waste piles, or processing operations; toxins may bioaccumulate in bats that consume prey carrying elevated loads of toxic constituents from mining effluent in their tissues; and indirect effects can occur if mining effluent reduces abundance of insect prey dependent on receiving waters. As stressed in other sections, C. townsendii is extremely vulnerable to degradation of habitat due to its high site fidelity and narrow roosting...
requirements. Thus, if uninformed mine closure, renewed mining at historic sites, and disturbance at cave roosts continue, the downward trend in Townsend’s big-eared bat abundance is likely to continue in Region 2 and elsewhere.

Fortunately, recognition that abandoned mines are valuable to Corynorhinus townsendii and other species of bats, spurred by concerns over declines of cave-dwelling bats (e.g., Henshaw 1972), has gradually prompted efforts to identify and protect such structures (e.g., Bat Conservation International’s North American Bats and Mines Project). A particularly good example of such a program at the state level is the Colorado Bats/Inactive Mines Project. Currently in its 16th year, the project, with the help of volunteers, has screened not less than 3470 mines, resulting in the installation or planned installation of gates at 535 mines (Navo et al. 2002).

Townsend’s big-eared bats showed higher fidelity to cave roosts than to mine roosts in the Great Basin (Sherwin et al. 2003), but cave roosts also showed little sign of human visitation. Elsewhere, caves with a high degree of accessibility to the public or those that are popular with cavers are likely to receive persistent levels of visitation within and between years. Even if the disturbance caused by visitations is minimal (which may well not be the case), Townsend’s big-eared bats may not use these caves because of frequent presence of humans, resulting in reduction of available habitat for Corynorhinus townsendii. For example, following several visits by recreationalists during the summer months, a maternity colony abandoned a site in the northern Black Hills that served as both maternity roost and hibernacula. The site’s hibernating population also showed declines, suggesting either additional visitations during winter (Tigner and Dowd Stukel 2003) or unwillingness of bats to return to a site that had experienced disturbance. It is also possible that abandonment of the site resulted in increased levels of mortality of adult or juvenile bats, which were in turn reflected by lower numbers of hibernating individuals.

Foraging habitat

Trends in foraging habitat are difficult to identify, in part because Townsend’s big-eared bat has been shown to forage in a wide variety of habitats. Conversion of native shrub and grasslands for urban development or for agriculture use probably alters the composition and abundance of the insect community, and it may lower the quality of foraging habitat if this shift reduces the prevalence of prey preferred by Corynorhinus townsendii. Draining or altering wetlands and loss of vegetation along riparian corridors may also reduce the quality of foraging sites.

Throughout its range, Corynorhinus townsendii forages heavily among the forest canopy and along forest edges. Thus, harvesting and burning of woodlands in close proximity to roosting colonies may reduce both the quantity and quality of foraging habitat. Pesticide spraying in these areas can also reduce prey availability and contribute to a build-up of toxins in bats if the pesticides bio-accumulate (O’Shea and Clark 2002).

Extrinsic threats

Disturbance and destruction of roosts

Townsend’s big-eared bats are notoriously sensitive to disturbance at roost sites (Kunz and Martin 1982). Many view disturbance at roost sites and elimination of roosting habitat through closure of abandoned mines to be the most serious threats to Corynorhinus townsendii in the West (e.g., Pierson et al. 1999, Hutson et al. 2001, Ellison et al. 2003a). Although few would argue what “closure of abandoned mines” means, disturbance is a general term that can encompass a wide range of activities. These activities may or may not be intended to destroy, harm, or displace bats or their roosting habitat. For the purposes of this document, we define disturbance as any human activity or action that is likely to disrupt the normal pattern of activity for C. townsendii such that chances of survival or reproduction are reduced. This definition has the advantage of being independent of intent or method, and it compels us to consider likely outcomes of a particular action, rather than to rely on knowledge that a particular action is or is not defined as a “disturbance.” Some actions are so blatant that they clearly constitute disturbance. Others, however, are more subtle and require consideration of context. Note also that although natural events such as fires, floods, mudslides, earthquakes, and ice ages all would (and should) constitute disturbance, we will focus on anthropogenic disturbance because, unlike “natural disturbances,” those that result from human activities are often systematic and chronic. Also unlike “natural disturbances,” human actions, particularly management activities, are generally within our control and fall within the purview of this document.

One common source of disturbance involves physical entry into a cave or mine that harbors bats. Although members of organized caving groups (e.g., National Speleological Society) are generally cognizant of the unique and fragile biota in caves and
promote responsible caving practices and protection of cave resources, so-called “amateur recreationalists” decrease the utility of roosting habitat through increased disturbance or arrant destruction (Barbour and Davis 1969). Uninformed explorers, or the simply curious, may not even be aware of the presence of bats inside, but the bats are certainly aware of them. Increased noise levels and the use of bright lights, if prolonged and severe enough, are likely to arouse resting bats to the point that they begin to fly inside the roost. If bats are discovered inside a roost, which is not unlikely given that Corynorhinus townsendii roosts exposed and often low on roost walls, attempts to touch or dislodge roosting bats will almost certainly initiate flight. In either case, for the curious who may have been unaware of the presence of bats, and for whom bats represent scary, evil creatures intent on getting tangled in hair, the sudden presence of flying bats in a confined, darkened space may illicit an aggressive response in “self-protection.” Clearly, such a scenario would be hazardous for bats and humans, particularly those unaccustomed to or unprepared for subterranean exploration.

Even when visitors do not venture far into the roost, the mere presence of humans in or near the mouth of roosts may be enough to disturb the bats roosting within (e.g., Graham 1966, Lacki 2000, Tigner and Dowd Stukel 2003). Increased noise levels, smoke and heat from campfires, and detonation of fireworks and firearms near or into the roost entry all clearly have the potential to disturb roosting bats. If groups are congregated near the roost entrance or close to emergence, bats may be hesitant to exit. For animals with high energetic demands that will not have had food or water for some 14 to 16 hours, delayed emergence, and therefore delayed access to food and water, takes on added significance.

Disturbance of roosting bats is cause for concern at any time, but disturbance at certain times and of certain types of colonies can be especially detrimental to the fitness of the bats. Disturbance of maternity colonies may result in roost abandonment by Corynorhinus townsendii (e.g., Lacki 2000, Tigner and Dowd Stukel 2003), and mothers that abandon roosts may leave non-volant young behind (Altenbach 1998). Unless the young are fully weaned and volant, their chances of survival are low. Disturbance at hibernacula can lead to unnecessary expenditure of vital energy reserves (Thomas 1995), and given the acute vulnerability of hibernating bats and the degree to which their tight energy budgets are already being taxed, disturbance at hibernacula may decrease chances of overwinter survival.

Vandalism at caves or mines, though perhaps less common than other forms of disturbance, may result in outright destruction of roosting bats. In one oft-related case, the largest known wintering western population of Corynorhinus townsendii was lost after arsonists set fire to support timbers in an abandoned mine (Tuttle and Taylor 1998).

Activities that occur outside the roost but that result in changes inside the roost also constitute disturbance. For instance, removal of vegetation near roost entrances can alter airflow and temperature regimes inside the roost. Given that Corynorhinus townsendii appears to select roosts based, in part at least, on these conditions (reviewed in Habitat requirements section), roosts may be rendered unsuitable following timber harvest, brush removal, prescribed burning, road construction, or other surface altering activities near roosts. In addition, actions that alter the flow of surface water can affect bats by flooding roosts or altering internal humidity levels (e.g., by creating or eliminating pools of water inside roosts). Moreover, any of these activities are also likely to change the quantity and quality of foraging or drinking habitat for the bats, which may exacerbate the effects of roost disturbance.

The ongoing reduction in roosting habitat facilitated by wholesale closure of mines throughout the West has likely magnified the negative effects of disturbance on bats in caves and mines (Altenbach 1998). Closure of mines, often done in the interest of public safety or for liability reasons, typically consists of blasting or backfilling openings (Altenbach 1998). Precise estimates of the number of abandoned mines in the West (or in Region 2) are difficult to come by, in part because definitions of what constitutes a mine vary from state to state and across federal land management agencies. According to a report sponsored by the Western Governor’s Association (Anonymous 1998): “Some consider multiple shafts and openings in one location as one mine, others consider each opening, shaft or disturbance a separate abandoned ‘mine’. As such, data...are not comparable among states and cannot be added together to create a westwide picture.” For the same reasons, estimating the number of these mines that have been closed is difficult, but it is probably safe to assume that the number is substantial. For instance, prior to recognition of the potential value of abandoned mines to bats, some 3,000 mines in Nevada were
closed without any type of wildlife surveys (Altenbach 1998). This practice has probably destroyed numerous hibernacula and/or maternity roosts (Altenbach and Sherwin 2002) and has undoubtedly destroyed roosts that *Corynorhinus townsendii* and other species of bats use intermittently.

**Pesticides and environmental toxins**

Pesticides may affect bats in two main ways: through bioaccumulation and through reduction in prey abundance. Several aspects of the life history of bats conspire to increase their vulnerability to exposure of pesticide residues even at low levels. Given that most North American bats are insectivores, application of pesticides over large areas of forest and agricultural lands likely decreases the abundance of insect prey. To the extent that application is concentrated in particular areas, local populations of bats that use these areas may be faced with increased foraging costs and commute times, or they may be at risk from direct exposure to the chemicals.

In western forests, efforts to control populations of pest species, some of which are lepidopterans (e.g., spruce budworm, gypsy moth), often include aerial application of pesticides. The pesticides tend not to be species-specific, and numbers of non-target species may be reduced substantially following application (Miller 1992). Because a significant proportion of the diet of *Corynorhinus townsendii* comprises lepidopterans (Whitaker et al. 1977, Burford and Lacki 1998), actions that reduce the local abundance of moths have the potential to affect local populations of *C. townsendii* negatively by reducing the prey base. This may lead to a shift in foraging areas as bats search for prey, and most likely will be associated with increased foraging costs. Generally, pesticides do not achieve 100 percent control; some targets survive, and after time populations of insects rebound. Unfortunately, some pesticides produce more enduring legacies.

Organochlorine pesticides (OCPs) and their residues probably have contributed to local or regional declines of bat populations (Clark 1988, 2001). Accumulation of OCPs, even at sublethal levels, poses risks to bats because they elevate metabolic rates in vertebrates. For bats, which have limited fat reserves, increased metabolism could be detrimental (Swanepoel et al. 1999), especially to mothers, young, and hibernating individuals facing intrinsic energy limitations. Although many of the OCPs that proved most harmful to bats (e.g., DDT, DDE, aldrin, dieldrin) have been banned or restricted in the United States since the 1970’s or early 1980’s, they continue to persist in the environment and may still be found in tissue samples from bats (e.g., O’Shea et al. 2001). Particularly grievous characteristics of once-common OCPs and their metabolites include their long residence time in the environment and their tendency to bioaccumulate in the food chain. Bats are especially susceptible to bioaccumulation because they are long-lived and forage at upper trophic levels. Moreover, the lipophilic nature of these contaminants results in their concentration in fat tissue. Hibernating bats rely on fat stores and thus risk mobilizing accumulated residues, and this is particularly so for lean versus fat individuals (Swanepoel et al. 1999). Hence, accumulation of OCPs may disproportionately affect young of the year because they generally enter hibernation with lower fat reserves than adults (Pearson et al. 1952).

It may seem counterintuitive to suggest that juveniles entering hibernation may have accumulated enough pesticide residue in the few months during which they forage on their own to put them at risk. Yet juvenile bats appear to be most susceptible. One explanation for this is that OCPs and their residues concentrate in milk, and young may therefore ingest high doses while nursing (Clark 1988). In one study, concentrations of DDE (the primary metabolite of DDT) in juvenile gray bats (*Myotis grisescens*) were two orders of magnitude greater (0.28 mg per kg compared to 34 mg per kg) 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. In addition, it appears that transfer can begin before birth. Newborns with detectable levels of DDE and DDT demonstrate that these pesticides crossed the placenta in 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 Kryniwsky 1978). What has been more difficult to establish is the extent to which such exposure compromises fetal development or offspring survival and growth. It would be valuable to understand if rates of reproductive failure vary with exposure level, or if there are threshold levels below which reproduction and development remain unaffected.

For males, at least, it appears that reproductive failure may in fact be one outcome of exposure to OCPs given that the androgen blocking effects of DDE can lead to interference with sexual development and fertility in males (Clark 1988). This may be cause for concern because, lacking the ability to export much of their residue load to juveniles as females do, concentrations of OCPs tend to be higher in adult
males than in adult females (Clark 1988). If the ability of males to sire offspring is compromised, and/or if juvenile males regularly experience interference with sexual development as a result of transfer of pesticide loads from mothers, then deleterious effects at the population level will likely result. Moreover, because mating occurs at hibernacula and therefore presumably involves bats from relatively disparate areas, lower reproductive output of females in areas without pesticide loads may be attributable to matings with reproductively compromised males. Yet, because of the temporal and spatial separation of the two events, it may be very difficult to attribute low reproductive success to such causes with any certainty.

In addition to pesticides, accumulation of various mining-related toxins (mostly heavy metals) in bats is highly probable in contaminated areas (O’Shea et al. 2000). Bats accumulate heavy metals in various tissues, and many are lethal in small quantities (O’Shea et al. 2000). Metals found in mine waste include cadmium and selenium, both of which bioaccumulate through the food chain and are teratogenic (O’Shea et al. 2000). In addition, other metals (e.g., aluminum, arsenic, cadmium, chromium, copper, lead, mercury, silver, zinc) found in mine waste are toxic to aquatic life and may thus result in reduction in prey availability (O’Shea et al. 2000).

Accumulation of heavy metals may occur through direct exposure and through consumption of contaminated insects or water. For example, where open-pit cyanide-extraction gold mining is common, bats are the most commonly recovered group of mammals found dead near the mining operations, probably from drinking from the surface of leach ponds containing cyanide-laced water (Clark and Holthem 1991). Not only do Townsend’s big-eared bats commonly roost in abandoned mines where they may be exposed to contamination, but renewed mining at historical sites is likely to liberate additional contaminants that would then be available for bio-uptake (O’Shea et al. 2000). Where renewed mining occurs in close proximity to old mines used by Corynorhinus townsendii and other species, there is high potential for increased levels of exposure or contamination through bioaccumulation. In such cases, mine operators should be required to make the ponds inaccessible (e.g., with protective netting) to bats and other species of wildlife.

**Targeted areas in Region 2**

As outlined above, extrinsic threats to Corynorhinus townsendii in Region 2 relate to roost disturbance and destruction, exposure to pesticides and mining related contaminants, and changes in landscape structure that alter energy budgets. Given that very few areas in Region 2 are immune to any of these threats, biologists and managers should strive to identify specific areas within their jurisdictions that are especially prone to such events, paying particular attention to areas that contain known or suspected occurrences of C. townsendii.

At the regional level, the Black Hills of South Dakota and Wyoming should be considered a high priority, given relatively intense resource extraction and recreational use, and the relative isolation of populations of Corynorhinus townsendii that occur there. Approximately 100 caves occur in or near the Black Hills where limestone outcrops appear at the surface. Two of these caves harbor thousands of Townsend’s big-eared bats during parts of the year (Tigner and Dowd Stukel 2003). In addition, approximately 900 abandoned mines exist in a four-county area around the Black Hills, 360 of which occur on USFS land (Anonymous 1998). Some or all of these mines may house C. townsendii or other species of bats at various times of the year.

**Intrinsic vulnerability**

As a group, bats are vulnerable to extirpation or extinction because of their unique life histories, notably their low annual fecundity. Townsend’s big-eared bat may be even more susceptible because of its wing morphology, restrictive roosting requirements, sensitivity to disturbance at roost sites, and the ongoing elimination of roosting habitat.

Like most insectivorous bats, Corynorhinus townsendii has low annual fecundity, producing at most one pup per female per year. However, females may forgo reproduction during poor years, and as a result, population growth rates may be even slower than projected. Given these constraints on reproductive output, it is very unlikely that populations can recover quickly from declines.

Because of its wing morphology, Corynorhinus townsendii is highly dependent on local habitat features (i.e., caves/mines, foraging areas, water holes, etc.), which makes them vulnerable to alteration and removal of these features. Indeed, aspect ratio, a component of wing design, is a significant predictor of extinction risk in bats (Jones et al. 2003, Safi and Kerth 2004). Low aspect ratio wing design increases extinction risk, most likely through its correlation with biological
factors that are the focus of extinction processes such as small home range, small colony size, limited dispersal capabilities, and low exchange of individuals among colonies (Jones et al. 2003). Wing design, then, provides a surrogate measure of extinction risk by linking morphology to biological processes that directly influence extinction risks.

The restrictive roosting requirements of Corynorhinus townsendii also contributes to their intrinsic vulnerability. The distribution of suitable roosts on the landscape is patchy, and C. townsendii tends to show high fidelity to particular sites. Hence, C. townsendii tends to abandon roosts in support colonies. It may also be difficult for C. townsendii to re-colonize patches of suitable habitat given their poor dispersal and migratory capabilities.

The now-common use of abandoned mines by Townsend’s big-eared bats may also contribute to their vulnerability. The movement of Corynorhinus townsendii into abandoned mines over the past 100 years or so may have led to an increase in the local or regional distribution of the species, but it apparently has not led to greater numbers of bats. Although it is not clear why the addition of roosting sites has not equated with increases in abundance (Altenbach and Sherwin 2002; reviewed above), the more dispersed nature of current distributions may increase extinction risks at the local level, particularly given ongoing removal of roosting habitat (e.g., through mine closure). As an analogy, consider a person hopping across a wide creek on emergent stones. Once across, if natural or other processes remove the stones, then the person is effectively cut-off from returning. If local distributions of C. townsendii became more spread out by “hopping” across the landscape “on” abandoned mines, as current patterns of distribution suggest (Sherwin et al. 2003), subsequent destruction of mines may effectively cut-off dispersal and migration between colonies. Such fragmentation may render local colonies more susceptible to extinction through stochastic variation in population cycles, variation and shifts in climate, and other processes that effect population dynamics.

Exacerbating vulnerability due to narrow roosting requirements, Corynorhinus townsendii is intolerant to roost disturbance and extremely susceptible to vandalism and destruction during hibernation. Disturbance at roosts may increase energetic costs and disrupt social structure if bats abandon roosts in search of other more secluded roosts. Sites to which C. townsendii have historically been faithful are likely separated by patches of unsuitable habitat. Therefore, the bats may be unaware of, or unable to reach, other suitable areas.

Vulnerability to disturbance is most pronounced for hibernation and maternity colonies, in part because of their reliance on torpor as a means of balancing energy budgets. Townsend’s big-eared bat uses shallow torpor outside of the hibernal period and deep torpor (i.e., hibernation) during the winter. The fact that temperate-zone bats in general, and Corynorhinus townsendii specifically, must rely on torpor reflects the tight energy balance under which they live. Disturbance during the maternal period may result in unnecessary energy expenditure, and disturbed maternity colonies may abandon the roost (e.g., Humphrey and Kunz 1976, Lacki 2000). If this occurs before pups are volant, then mothers may simply abandon their pups (Altenbach 1998). Hibernating individuals are especially vulnerable because disturbance during hibernation can cost bats up to 68 days worth of crucial fat reserves during arousal (Thomas 1995) and because they are essentially helpless until they can raise body temperature enough to attempt flight or escape, which may take up to an hour (Thomas 1995). As one account relates:

“At Carter Caves State Park, Kentucky, in the winter of 1957, hundreds of bats were killed by being stoned from the low ceiling. In December of 1958, vandals discharged fire crackers and homemade bombs in the midst of the clusters. On December 26, 1960, three boys, moments before our arrival, tore great masses of bats from the ceiling and trampled and stoned the helpless animals. Thousands fell into the stream which flows through the cavern and were drowned before they could rouse from their torpid state. An estimated 10,000 bats were killed.” (Mohr 1972).

Fortunately, reports such as this one are rare. However, they are not so rare as to dismiss this one as the isolated actions of a few miscreants. Other similar reports exist (though one is particularly disturbing for the wanton nature of the actions and magnitude of mortality), and many others are probably not witnessed or documented at all. Even when events are documented, they might not be reported widely. For instance, an account on the website of the California Department of Fish and Game (http://www.dfg.ca.gov/watchable/bats2.html) chronicles:

“caves and mines [used for ‘parties’] frequently strewn with beer cans, shotgun shell casings, fireworks, or other litter, [and] evidence of
cruel vandalism in the form of hair spray cans, matches, and incinerated bats [being] not uncommon in easily accessible caves and mines.”

Another case that, to our knowledge, has never been “officially” published involved the destruction and loss of the West’s largest known wintering population of Corynorhinus townsendii after arsonists entered a mine where the bats were hibernating and set fire to the support timbers (cited in, among others, Tuttle and Taylor 1998). These events, and others like them, illustrate starkly the extreme vulnerability of hibernating bats.

Management Implications and Potential Conservation Elements

Because adult survival appears to be key to maintaining viable populations of Corynorhinus townsendii (see Life history model), conservation efforts focused on protecting bats from extrinsic harm (e.g., disturbance or destruction at roosts) appear likely to yield the greatest benefits to this species. Given the acute vulnerability of hibernating bats to disturbance, protection of hibernacula should be of prime importance. Although fertility was not identified as being the most sensitive life history variable affecting population dynamics, reproduction rates clearly will affect population dynamics. Thus, adequate protection of maternity roosts will serve the dual function of minimizing human-caused mortality and, all else being equal, of maximizing reproductive success.

Protection of roosting sites, however, without regard to other landscape elements that are important to Corynorhinus townsendii may result in less than optimal results. Therefore, protection of foraging and drinking sites must also be considered as these elements contribute to energy and water balance in bats. Finally, other extrinsic threats (e.g., exposure to environmental toxins) likely threaten the long-term persistence of C. townsendii and other species of bats, and the greater the degree to which the negative effects of such threats can be mediated the greater the likelihood that viable populations can be maintained.

Roosting sites

Roost destruction and disturbance represent the most persistent and serious threats to Corynorhinus townsendii. Authors treating the conservation status of C. townsendii and other cave-dwelling species invariably implicate degradation of roosting habitat through disturbance and elimination of roosting habitat through mine closures in observed population declines (e.g., Tuttle 1979, Pierson et al. 1999). Uninformed closure of abandoned mines eliminates current or potential roosts, further fragments the landscape with respect to roosting habitat, and potentially increases the degree of isolation that colonies experience. This situation is exacerbated when increased disturbance at roosts compels bats to abandon sites. Thus, roosting sites are arguably the most important conservation element for C. townsendii in Region 2 and elsewhere.

Based on the relative value of particular types of roosts to various life stages of Corynorhinus townsendii and on the relative value of those life stages to overall population viability, we consider hibernation roosts to be of highest conservation priority, followed by maternity roosts and bachelor roosts. Hibernacula represent vital refugia from periods of severely reduced food supplies and below-freezing temperatures, and they are critical to the year-to-year survival of bats using them. Moreover, they are presumed to be relatively rare on the landscape. Maternity roosts are crucial components contributing to reproductive success, and therefore they clearly factor into local population stability and viability.

The value of abandoned mines to the populations of Townsend’s big-eared bat that use them is also considered high, particularly if traditional roosting habitat in caves has been compromised. Colonies that may formerly have roosted in caves may now be dispersed among abandoned mines, and rates of mine closure have been increasing (Meier and Garcia 2000). Therefore, efforts to identify and protect mines used by Townsend’s big-eared bat and other species of bats should be considered important components of a conservation strategy.

Foraging sites

Foraging habitat for Townsend’s big-eared bat typically consists of shrub and woodland habitat that harbor high abundances of moths and other insects. Foraging often occurs along the interface of two or more habitats. Although Corynorhinus townsendii appear to avoid large, open areas and areas of dense, regenerating forests, estimates of canopy coverage necessary to create suitable foraging conditions are unknown. It is likely that a mosaic of habitat conditions (e.g., mid- to late seral forest stands, riparian-shrub and grassland-shrub habitats) in close proximity to roosts will provide the necessary suite of conditions to allow C. townsendii to efficiently meet energetic demands (e.g., Wunder and Carey 1996).
Based on wing and echolocation morphology, *Corynorhinus townsendii* is expected to forage in more cluttered habitats and to avoid foraging in open areas (e.g., Aldridge and Rautenbach 1987). Like other species of bats, *C. townsendii* probably forages opportunistically by exploiting concentrations of insects, and it likely forages heavily in riparian areas (Fellers and Pierson 2002), around wetlands, and in the lee of forest edges or ridges where insects concentrate (Lewis 1970). Foraging sites that have dense and structurally diverse vegetation may support greater abundances of insect prey and provide escape from potential avian predators. Foraging sites that offer these characteristics are likely to be preferred to those that do not.

Very few studies have fully elucidated ecological responses of bats to changes in quantity or quality of foraging sites, and none has focused on *Corynorhinus townsendii*. This is not surprising given the large number of potential factors (and their interactions) that likely influence the attractiveness of foraging sites for *C. townsendii* and other species of bats, and given the limitations inherent in observational studies. Although we can be fairly certain that some actions will decrease the utility of foraging areas for *C. townsendii*, the relative contribution of any of them, or the combined effects of more than one, are difficult to predict *a priori*. In part, this is because any single action that alters foraging habitat is likely to do so in multiple ways, resulting in confounding effects. For example, removal of vegetation at foraging sites may:

- Reduce overall prey abundance
- Shift availability of particular prey species
- Alter how efficiently *C. townsendii* is able to forage at the site
- Alter the number of species competing for insects at the site.

In addition, “removal of vegetation” can occur at varying degrees (e.g., overstory versus understory removal, selective harvest, clear-cut harvest), each of which is likely to affect overall quality of foraging habitat differently.

**Drinking sites**

Like most animals, bats must drink water to maintain water balance. Bats drink by skimming the surface of calm water bodies, and they appear to avoid open water with too much clutter (i.e., vegetation). Local or physiological conditions may increase the reliance of bats on sources of open water. For example, bats that live in arid environments (e.g., much of the western United States) and lactating females are likely to depend even more on water sources than other bats. Therefore, maintenance of wetland and riparian habitats and other sources of open fresh water (e.g., water impoundments) at local scales should be considered an important conservation element. Drinking sites located near either roosting or foraging sites should be maintained, but drinking sites that are contaminated with heavy metals or other pollutants pose a serious danger to bats and other species of wildlife that drink from them, and bats should be excluded from using these sites until remediation can occur.

**Landscape context**

Roost, foraging and drinking sites each constitute only one piece of the puzzle necessary for conserving *Corynorhinus townsendii*. All three of these are required in a suitable spatial arrangement, so increasing the probability of long-term persistence of *C. townsendii* in Region 2 will require managing for all of these habitat components in concert.

Because *Corynorhinus townsendii* does not travel very far from roost sites to forage or drink, maintenance of foraging and drinking habitat within close proximity to roosts may be necessary to support colonies using those roosts. Accessibility to foraging and drinking sites can be enhanced if patches of suitable habitat connect those components and roosts. That is, habitat features that function to decrease flight costs (e.g., wind), to decrease risk of predation, and provide foraging opportunities are likely to benefit local populations.

The size of an area necessary to sustain colonies is difficult to predict, and ultimately it will depend on several site-specific factors, including availability of water, abundance of insect prey, time of year, reproductive status of the bats, and size of colony. Nonetheless, actions that tend to increase the fragmentation of a particular landscape are likely to affect bats by increasing energy expenditure and decreasing availability of prey, and such actions are likely to reduce the carrying capacity of an area. Removal of streamside vegetation through logging or grazing practices, removal of mid- to late-successional vegetation through logging or burning, and conversion of native shrub and grassland habitat through urbanization or other land-use practices are likely to increase fragmentation and negatively impact populations of *Corynorhinus townsendii* and other species of bats.
in Region 2. Actions that lead to fragmentation at the scale at which *C. townsendii* uses the landscape must therefore be avoided or minimized. Based on published estimates of the size of foraging areas used by *C. townsendii*, a maternity colony may require up to 260 ha (650 acres); however, this number is for eastern populations, and area requirements may be lower in the West due to the generally smaller size of colonies. Conversely, water may be more limiting for western populations than for those in the East. Availability of fresh drinking water is necessary for bats, particularly lactating females because they export water in the form of milk. Thus, areas may need to be larger if bats must travel substantial distances to find water.

**Exposure to toxins**

Bats’ long life spans, combined with the long residence time of pesticides in the environment and bioaccumulation in the food chain, suggest that chronic long-term exposure and accumulation are likely to occur. High levels of organochlorine pesticides and residues in fat and brain tissue have been linked to precipitous declines of some cave-roosting species of bats (Clark 2001), and there is no reason to suspect that *Corynorhinus townsendii* is less susceptible to the effects of pesticide exposure than other species of bats. In addition, the propensity of *C. townsendii* to roost in abandoned mines means that they may more readily come into contact with mining associated toxins, particularly heavy metals. The accumulation of such toxins in the food chain and consumption of toxin-laced water pose considerable dangers (O'Shea et al. 2000). Given the acute and chronic levels of poisoning, and the teratogenic and mutagenic consequences of exposure to many mining-related contaminants (O'Shea et al. 2000), it is important that exposure to these toxins is minimized. This may require remediation, and because of the large number of abandoned mines on the landscape, it will likely take considerable time. Permitting of new mines, or for renewed mining at historic sites, should include provisions to ensure that operators do not leave behind toxic waste.

**Tools and practices**

In this section, we discuss available tools and practices that may be employed to foster conservation on *Corynorhinus townsendii* in Region 2. We first discuss the value of education in the conservation of Townsend’s big-eared bat, and follow with a section to familiarize the reader with basic methodology and timing of Inventory and monitoring efforts. The knowledge from such surveys is critical to effectively implementing conservation measures outlined in the subsequent section on Population and habitat management.

**Education**

Few groups of vertebrates are so widely misunderstood and reviled as bats. Despite valuable ecosystem services provided by bats (see discussion in Symbiotic and mutualistic interactions section), many people are unaware of the value of robust populations of bats. Worse, age-old myths that portray bats as rabid, blood-sucking animals intent on getting tangled in the hair are slow to fade. Bats are often assumed dangerous vectors of several diseases (see discussion in Parasites and disease section), a misconception that, despite evidence to the contrary, is all too often parroted by the media and public health officials (Olnhusen and Gannon 2004). These and other misconceptions hamper effective conservation (Fenton 2003) and may result in hostility toward bats (see discussion in Intrinsic vulnerability section). Therefore, education should be a fundamental component of a conservation strategy for Townsend’s big-eared bat.

It is beyond the scope of this document to outline an education program for bats. However, we provide suggestions regarding what such a program should include and list some avenues of educational information and pre-existing educational programs that could be mustered.

A strong educational program would include components that:

- describe the beneficial role and ecosystem services that bats provide
- debunk baseless myths (especially regarding disease) that lead to vilification of bats
- explain the slow reproductive rate and fragile nature of bat populations and their habitat
- describe the diversity of bat species and their unique biology and morphology.

The forms in which these components may be conveyed to the public are varied. Interpretive trail signs may be used where caves or mines receive heavy and persistent public visitation. Signs could outline the reasons for treading lightly in caves and the penalties for vandalism. Trail signs are not recommended for caves or mines that are relatively secluded and receive little visitation.
Posters, brochures, and other printed materials can be distributed to interested members of the public at local events, from local USFS offices, or in conjunction with other education- or conservation-related presentations to the public; a wealth of such materials is available from Bat Conservation International (www.batcon.org). Informational talks can be very effective and offer the opportunity for interaction with the audience. For example, one of us (JG) regularly gives talks to groups of school-aged children, and regularly discusses bats with the general public. In most cases, questions arise revolving around the myths mentioned above and can be discussed and dispelled immediately.

Those developing an education program will benefit from investigating existing education programs such as the USFS Conservation Education Program (http://www.na.fs.fed.us/spfo/ce/) or similar programs in other agencies and organizations. Additionally, conservation education partnerships with other agencies and organizations can provide a greater resource base, increase access to the public, and may carry greater weight than conservation messages endorsed by a single agency. Those integrating bats into pre-existing education programs will benefit from information and materials available from Bat Conservation International and from soliciting input from local experts (e.g., members of state chapters of the Western Bat Working Group).

**Inventory and monitoring**

Our goal in this section is to familiarize the reader with basic methodology and timing of various types of surveys for bats, along with the information that may or may not be gleaned from such surveys. It is not our intent, nor is it within the purview of this document, to expound in detail all of the considerations and caveats regarding particular survey methods. Suffice to say, unbiased sampling methods for bats are particularly difficult because of their unique biology (O’Shea and Bogan 2003), and this may affect results and the interpretation of survey efforts. For example, although all sampling methods have biases, those associated with acoustic and capture surveys of bats are such that estimating them is often impossible. We can be fairly certain that both capture and acoustic surveys do not sample all groups of bats consistently, but we are unable to quantify the degree to which this occurs (O’Shea and Bogan 2003). Several aspects of the biology of *Corynorhinus townsendii* make it a particularly difficult species to survey with these methods. First, because it is a slow flying, highly maneuverable bat, *C. townsendii* is adept at avoiding mist-nets. Second, the echolocation call of *C. townsendii* is relatively quiet, which means that acoustic surveys may fail to detect the bat when it is present.

It is also not our intent in this section to provide specific instruction on surveying for bats. Effective sampling often requires specialized skills, experience, and equipment that may not be readily available. Moreover, many biologists will simply not have the time or the mandate to engage in these activities. Those interested in a more thorough discussion of these topics are encouraged to consult any of the excellent references listed below by topic, especially Kunz and Kurta (1988) and O’Shea and Bogan (2003). In addition, state chapters of the Western Bat Working Group will be able to provide specific guidance on the details of planning inventory and monitoring programs in specific areas.

**General methods**

Three main methods are recommended to survey for bats: capture surveys, acoustic surveys, and visual surveys (Kunz and Kurta 1988). Capture surveys necessarily include disturbance and handling of bats. Acoustic surveys passively record the presence of bats as they echolocate in flight. Human observers can perform visual surveys with or without the aid of optical equipment and electronic devices. Each method has advantages and limitations, and each may be used in conjunction with others. The exact method or combination of methods used will depend on the question or questions of interest. However, surveys should follow existing standard protocols (e.g., Navo 1994, Altenbach et al. 1999, Tuttle 2003) and be designed to occur within roughly the same period during each occurrence to minimize differences attributable to intra-season variability in numbers. Because Townsend’s big-eared bat may switch among several different roosts within a season (Sherwin et al. 2003), surveys should attempt to identify and include nearby alternative roosts. If successful, results from such efforts will be important for understanding movement patterns and may provide predictive and conservation value if movements can be correlated with biotic and/or abiotic conditions.

Capture surveys are most often conducted with mist-nets or harp traps (Tuttle 1974). Because capture surveys necessarily involve handling of bats, information on species, age (Anthony 1988), and sex of captured bats can be collected, as well as data on morphological characteristics (e.g., size and weight) and reproductive status (Racey 1988). However, because *Corynorhinus townsendii* can easily avoid mist-nets erected at foraging and drinking sites, they may not be
captured during such surveys even if they are present. Therefore, a combination of capture and acoustic surveys may be employed to maximize the probability of detecting *C. townsendii*. Another consideration is that because of the level of disturbance associated with capture surveys, bats captured in mist-nets or harp traps may subsequently avoid these areas. Therefore, capture surveys may be used to establish baseline estimates on species composition and demographic profiles of the species, but repeated capture surveys at roosts or foraging/drinking sites should be avoided.

Acoustic surveys typically employ some type of ultrasonic detector, and are appropriate for detection of the presence of bats, but may not be appropriate for species discrimination (e.g., see Barclay 1999, O’Farrell and Gannon 1999, O’Farrell et al. 1999, and Fenton et al. 2001). Acoustic surveys are not appropriate to estimate size of colonies because the number of bat calls recorded is not a reliable indicator of number of bats. That is, one cannot be sure whether 10 bat calls represents 10 bats or 1 bat flying by the detector 10 times.

Visual surveys are generally effective only at known or suspected roosts, and may be used to estimate colony size provided that only one species of bat is using the roost. Experienced workers may be able to roughly differentiate species by size or flight characteristics, but if species composition is unknown, or when large numbers of bats exit, this method is highly prone to error in species identification and/or individual counts. Visual counts may be conducted internally or externally. Internal counts require entry into a cave or mine, and therefore are generally limited to situations where the safety of surveyors is not compromised by structural inadequacies. Where safe entry and exploration of a cave or mine is questionable, external surveys may be conducted in lieu of internal surveys.

The accuracy of counts using human observers will vary with observer experience, number of bats present, and amount of vegetative clutter surrounding the exit, all of which are likely to influence the number of bats seen and recorded. The effectiveness of human observers may be increased with the use of specialized optics (e.g., night-vision scopes and infrared cameras). 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).

### Location

For cavernicolous species of bats, surveys may be conducted either at known or suspected roosts, or at foraging or drinking sites. Because bats roosting in caves or mines are more spatially aggregated within the roost and as they exit the roost than they are during foraging bouts, internal and/or external surveys at roosts are generally necessary to determine colony size and type. Capture and acoustic surveys are often conducted at suspected drinking and foraging sites, and they are generally appropriate to determine which species are present in an area or to determine use of foraging areas. Note, however, that use of acoustic surveys for identification beyond the generic level requires specialized skills and experience, and this type of survey is generally more appropriate for comparing levels of activity among sites.

If capture surveys are deemed to be warranted at roost sites (e.g., at the mouth of a cave or mine), then mist-nets should be avoided, especially if the roost harbors large numbers of bats (ASM 1998). Mist-nets require constant vigilance. Bats captured in nets struggle to free themselves, and safe removal of the bats, even by experienced workers, may take several minutes. During this time, many more bats are likely to become entangled, especially if the net or nets completely cover the roost opening. In such cases, harp traps are the recommended alternative (ASM 1998). Although harp traps must be monitored, they do not require constant attention, and because bats are funneled into a collection bag, they are less prone to injury or predation than those ensnared in mist-nets.

Regular surveys at hibernacula may provide reliable information on long-term population trends because hibernacula tend to be relatively permanent and to 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), surveys should be conducted biennially. Navo (1994, 1995) and Altenbach and Milford (1995) describe methods and timing for surveys for bats at mines.

Bats emerging from maternity or bachelor roosts may be surveyed 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 they
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 use of night-vision equipment may increase the effectiveness of human observers. 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 can allow 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, and it does not involve capture or handling of bats. 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 their utility.

**Timing**

Capture and acoustic surveys must occur during periods of bat activity and therefore are conducted at night. Capture surveys begin near sunset and may or may not run all night. Bat activity is usually highest in the hours following sunset, so surveys designed to run for a set period (e.g., 4 hours) may yield the largest return per unit effort. External capture and visual surveys at roosts also occur during the evening, but once bats have left the roost to forage, surveys may be considered complete if the goal of the survey is to estimate colony size.

Internal surveys at warm season roosts to determine colony size should occur just prior to and following parturition, when numbers of bats are likely to be most stable. Internal surveys will require specialized training, skills, and equipment. Internal surveys in mines require even greater precaution and experience because abandoned mines are often structurally unstable, may contain poison air and toxic waste, and may have unmarked shafts that drop precipitously. Only qualified personnel should conduct internal surveys of abandoned mines. Once a roost site has been identified, abundance estimates of bats using the site may be obtained by internal visual counts, visual counts of exiting bats, or by deploying passive infrared or night-vision optics near the entrance to record exiting bats. External surveys are preferred in order to minimize disturbance at maternity roosts (ASM 1998).

Because *Corynorhinus townsendii* are generally inactive during the winter, internal surveys will likely be required. These surveys are subject to the safety considerations mentioned above. Surveys to establish use of a cave or mine may be conducted after bats have begun to disperse to hibernation site (generally from mid-September). Surveys to estimate colony size should occur during the coldest months, when numbers within the roost are likely to be most stable.

Results from the Great Basin (Sherwin et al. 2000a, 2003) indicate that colonies of *Corynorhinus 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 (Table 12). Sherwin et al. (2003) modeled lability in roost occupancy by big-eared bats 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 percent probability whereas maternity colonies typically used a single cave for the duration of the maternity season and among years. A minimum of nine surveys was required to eliminate a mine as a bachelor roost whereas only three surveys, on average, were needed to eliminate a cave as a bachelor roost with 90 percent probability. Potential hibernacula required at least eight surveys to be 90 percent sure that they were not used, but large colonies (≥ 5 individuals) show greater fidelity than small colonies (<5 individuals), with large colonies requiring a minimum of two surveys, and small colonies requiring at least 10 surveys.

**Population and habitat management**

The life histories of bats 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 and conservation strategies for *Corynorhinus townsendii* focus on increasing habitat (particularly roosting habitat) as a means of increasing numbers of bats (e.g., U.S. Fish and Wildlife Service 1979, Pierson et al. 1999, Altenbach et al. 2002). Since adding new, high-quality roosting
habitat for Townsend's big-eared bat is likely not a feasible management tool, particularly at large scales, management efforts should focus instead on improving roosting conditions at existing roost sites, stemming the loss of current roosting habitat, and insuring that future potential habitat (e.g., mines slated for closure) are available to bats.

Compared to the steady recruitment of snags used by many forest-dwelling species of bats, cavernicolous structures (particularly caves) are not rapidly being created on the landscape. Although ongoing mining activities may continue to create subterranean habitat, it is unclear whether the rate at which new mines are opened is equal to closure rates. Also unknown is how long new mines will sustain active mining. Because Townsend’s big-eared bats are not likely to use active mines, they remain unavailable as roosts until they are abandoned. In addition, renewed mining at historic sites is likely to displace any bats that may have been using the mine while it was abandoned. Thus, the primary focus of maintaining suitable roosting habitat for Townsend’s big-eared bats is currently through protection of underground roosts that are available at this time.

There are two primary means by which cavernicolous roosting opportunities are decreased, mine closure and ongoing disturbance at caves and mines by human activity. Managers must first identify caves and mines that bats currently use. This is important because mine closures are steadily increasing and often occur in the absence of bat surveys (Altenbach 1998, Meier and Garcia 2000) and without consideration of their current or potential value for bats. Mines slated for closure should first be evaluated for the presence of bats and for their potential as suitable roosting habitat. Suitable mines should then be closed in a way that allows for bat use and should be safeguarded against human disturbance. Where concerns for public safety surround used or potential mine roosts, gating or other methods of excluding the public from the site (e.g., closure of roads or trails leading to the roost) may provide viable alternatives. Eliminating disturbance at cave and mine roosts through seasonal restrictions or gating will also protect roosting habitat. Townsend’s big-eared bat is highly intolerant to human disturbance at roosts (e.g., Pearson et al. 1952, Graham 1966, Humphrey and Kunz 1976, Pierson and Rainey 1998). Thus, seasonal or permanent restrictions may be required for caves or mines that are deemed important as hibernacula or maternity roosts. Closures may be “hard” (e.g., cave or mine gating or road closure) or “soft” (e.g., voluntary compliance with closures that are clearly indicated with signs at trailheads). As mentioned below in Protection and conservation of roosting sites section, the Federal Cave Resources Act and Subpart B Orders provide tools with which land managers can protect important caves and mines.

While the previous paragraphs in this section have emphasized identification and protection of all roosts (i.e., maternity, hibernation and bachelor roosts), we must stress the importance of hibernation roosts in the population management of Townsend’s big-eared bats. Hibernacula play a central role in the year-to-year viability of the populations of bats using them because the ability to use energy stores as efficiently as possible is absolutely crucial to the survival of overwintering bats.

During hibernation, Corynorhinus townsendii is most vulnerable to disturbance and to fluctuations in ambient conditions. Caves or mines with shafts that are deep enough to buffer bats from fluctuations in temperature and that maintain high levels of humidity and moderate airflow are necessary for efficient hibernation and overwinter survival. Roosts that provide this suite of conditions are likely to be relatively rare and highly valuable to the bats that use them. For these reasons, identification and protection of hibernacula should be considered a prime objective in any conservation strategy for C. townsendii.

Finally, although it is important to maintain and protect as many suitable roosts as possible across the landscape, baseline data on abundance and population densities are required to evaluate population trends adequately and to determine the effects of various management decisions on bats. Given the lack of baseline data on historical population sizes, it is imperative to initiate systematic surveys to establish these data for current populations.

Because effective management of Corynorhinus townsendii depends on an understanding of its abundance and distribution, and because land management agencies must spread limited conservation dollars among many competing programs, agencies may benefit from involving the public to the extent practicable. Local caving groups represent a potentially under-appreciated source of information about the presence of bats in caves and mines. These groups often maintain information about the location, condition, and complexity of caves; the extent of human visitation at caves; and how conditions in the cave have changed through time (Altenbach and Sherwin 2002). Considering the number of potential roosts that might
yearly be visited by cavers and the general willingness of such groups to protect both caves and their biota, involvement of these organizations has the potential to greatly increase our understanding of the distribution of *C. townsendii* and the size of local populations (see Table 13 for a list of these groups in Region 2 and contact information).

**Protection and conservation of roosting sites**

Safeguarding roosting habitat is the first step to take toward maintaining viable populations of *Corynorhinus townsendii* in Region 2. Protection of known roosts, particularly those with significant roosting colonies, will most effectively help to achieve this goal. Within Region 2, *C. townsendii* relies primarily on caves and abandoned mines for roosting habitat, and therefore, we focus our attention on the means by which caves and mines may be protected.

The most imminent threat associated with mines and bats is closure of mines in the interest of public safety. Typically, mines are closed by blasting and backfilling, and often with no pre-closure survey to assess mine use by bats (Altenbach 1998). Mine protection begins with pre-closure surveys intended to identify use by bats and, if warranted, construction of bat-friendly gates on mines that are important to bats, but that are deemed threats to public safety. Although caves may not present the same level of public safety concerns as mines, they often receive high levels of recreational use. Caves that harbor colonies of bats and that receive high levels of human visitation must be protected to ensure long-term use by bats.

**Identification of sites:** The first step in protecting important roosting sites is to learn where they are. While some hibernation and maternity roosts are known from Region 2, it is likely that others remain undiscovered by management agencies. Therefore, regular systematic surveys should be initiated to identify important roosting sites. Making such surveys efficient is a potentially difficult task requiring advanced planning. At a large scale, our current understanding of *Corynorhinus townsendii* distribution is depicted in Figure 4 and Figure 5. Further, Colorado, South Dakota, and Wyoming have produced state-wide predictive distribution maps (Figure 6, Figure 7, Figure 8), but these maps likely over-predict distribution and have limited utility at local scales. Managers and biologists can obtain more detailed information by contacting local Natural Heritage Programs and/or Bat Working Groups for occurrence and distribution information in their area. Within areas that *C. townsendii* could inhabit, survey focus should be given to locations with known karst geology (i.e., those likely to contain concentrations of caves) and to areas with abandoned mines. Consultation with federal or state representatives of abandoned mine land reclamation programs may be necessary to identify mine locations, and such interagency cooperation can also help to prioritize surveys of mines slated for closure.

Once important roosts are identified, protection of roosting habitat requires minimizing or eliminating human disturbance at roosts, preventing closure of abandoned mines that are important to bats, and ensuring that surface disturbing activities are done at appropriate times and at appropriate distances from roosts. Several pieces of legislation are available for protection of caves and mines. In some cases, it may be enough to protect important roosts through these or other pieces of legislation. In others, legislation may serve as a precursor to physical measures to restrict entry or access to important sites.

**Legal protection of roosting sites:** The legislative acts highlighted below may be viewed as those most likely to be useful for the protection of caves and mines on federal lands. However, the list may not include all pertinent federal, state, or local legislation, and we encourage managers and biologists to familiarize themselves with relevant laws and regulations in their own jurisdictions.


“*A 'significant' cave is defined as a cave located on Federally administered lands that has been evaluated and shown to possess features, characteristics, values, or opportunities in one or more of the following*”

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1 A useful resource for cave management on USFS lands is published by Umpqua National Forest (UNF 2004), from which much of this information on legislation is derived.

2 Also known as the Cave and Karst Resource Protection Act of 1988.
Table 13. List of local affiliates of National Speleological Society (grottos) in USDA Forest Service Region 2. No information for grottos was available for Nebraska. Note that this list likely does not represent an exhaustive compilation of all such groups in Region 2.

<table>
<thead>
<tr>
<th>Grottos in Colorado</th>
<th>Grottos in or near Wyoming</th>
<th>Grottos in or near Kansas</th>
<th>Grottos in South Dakota</th>
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</thead>
<tbody>
<tr>
<td>Colorado Grotto</td>
<td>Armpit Grotto</td>
<td>Kansas Speleological Society</td>
<td>Paha Sapa Grotto</td>
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<tr>
<td>c/o Gerry Forney</td>
<td>c/o Carol Uhl</td>
<td>c/o Wayne White</td>
<td>c/o Rene Ohms</td>
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<tr>
<td>680 Emerson St</td>
<td>P.O. Box 244</td>
<td>419 S. Maple Newkirk, OK 74647</td>
<td>1212 Sherman St</td>
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<tr>
<td>Denver, CO 80218-3216</td>
<td>Laramie, WY 82070-0244</td>
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<td>Hole-in-the-Wall Grotto</td>
<td>Boston Mountain Grotto</td>
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<td>c/o Fred Luizer</td>
<td>c/o Robert Montgomery</td>
<td>c/o Uncle Sam’s S. Outfitters</td>
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<tr>
<td>2510 Taft St No. 210</td>
<td>P.O. Box 2102</td>
<td>1494 N. College</td>
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<tr>
<td>Boulder, CO 80302</td>
<td>Casper, WY 82602</td>
<td>Fayetteville, AR 72703</td>
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<td>Northern Colorado Grotto</td>
<td>Bear River Grotto</td>
<td>Kansas City Area Grotto</td>
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<td>c/o Frank Leskinen</td>
<td>c/o Thomas Haskett</td>
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<td>Southern Colorado Mountain</td>
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<td>c/o Jon Barker</td>
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<tr>
<td>2220 W Platte Ave</td>
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<tr>
<td>Colorado Springs, CO 80904-3452</td>
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<td>Timberline Grotto</td>
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<td>c/o Kenneth Newton</td>
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<td>4399 CR 243</td>
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six resource areas: biota, geologic-mineralogic-paleontologic, cultural, hydrologic, recreational, or educational-scientific.”

This act can affect protection of caves and cave resources in three main ways:

- by limiting public availability of information about locations of caves on federal lands
- by prohibiting any act that interferes with free movement of animals within a cave
- by prohibiting what could broadly be termed “vandalism” of the physical structure at a significant cave.

The FCPRA is probably the strongest legislation available to management agencies for the protection of caves that do not harbor endangered species (which organisms would qualify for legal protection under other legislation). In addition to this legislation, the Forest Service Manual (FSM 2004, as amended), Title 2300, Chapter 2350, Section 2356 concerns Cave Management and provides legislation under the authority of Title 16 of the United States Code (U.S.C.). Legislative measures provided in the Forest Service Manual include:

The Organic Administration Act of June 4, 1897 (16 U.S.C. 551) – Authorizes protection of cave resources from theft and destruction (36 CFR 261.9a, 9b, 9g, and 9h), classification for special interest areas that are managed for recreation use substantially in their natural condition (under 36 CFR 294.1), and special closures under 36 CFR 261.53 to protect threatened cave resources.

Antiquities Act of 1906 (34 Stat. 225; 16 U.S.C. 431 et seq.) – Authorizes criminal sanctions for destruction or appropriation of antiquities. Scientific investigations of antiquities on Federal lands are permissible subject to permit and regulations. Uniform rules and regulations pursuant to this Act are in Forest Service Manual 1530.12.

Archaeological Resources Protection Act (ARPA) October 31, 1979 (16 U.S.C. 470aa) - Clarifies and defines “archaeological resources,” which may include caves and potentially mines. The Act authorizes confidentiality of site location information and permit procedures to enable study and investigation of archeological resources on public lands by qualified individuals. This act may be appropriate to afford some protection to mine sites if various pieces of equipment used in mining or the presence of historic structures either in or near the mine can be demonstrated to have importance to the nation’s development (Olson 2002).

All of these acts may be effective tools for the protection of caves and cave resources, but their suitability for protecting mine roosting habitat appears to be quite limited. Clearly, the protection of caves is an important aspect of a conservation strategy for Townsend’s big-eared bat. However, mines are frequently used by and important to Corynorhinus townsendii, and protection of mines currently or potentially used as roosting habitat should receive appropriate consideration.

If necessary, protection of mines on USFS lands may be provided under so-called Subpart B Orders. Issued under authority of Section 36 of Code of Federal Regulations, these orders are legally enforceable, can be issued quickly, and allow the flexibility to effect seasonal or permanent closure as needed (Nieland and Meier 2002). Specifically, Title 36 (C.F.R.), Subpart B, Sec. 261.53 specifies that:

“When provided in an order, it is prohibited to go into or be upon any area which is closed for the protection of:

(a) Threatened, endangered, rare, unique, or vanishing species of plants, animals, birds or fish.
(b) Special biological communities.
(c) Objects or areas of historical, archeological, geological, or paleontological interest.
(d) Scientific experiments or investigations.
(e) Public health or safety.
(f) Property.”

It is further specified in Sec. 261.51 that closures, restrictions, and other prohibitions issued by such orders be posted in form and location to “reasonably bring the prohibition to the attention of the public.”

Hibernacula should be closed to human visitation and entry during the hibernation period (approximately November 1-April 1). Visitation can be discouraged by posting signs near trailheads or other access points indicating that the cave or mine is closed for the protection of hibernating bats. If necessary, closure can be enforced with the construction of bat-friendly gates at or near the roost entrance (e.g., Ellison et al. 2003a). Seasonal restrictions (April 1-September 1) of known maternity roosts are recommended. Restrictions may be effected in the same manner as above.
If, after such protections have been enacted, visitation, vandalism, or other disturbance continues, then physical means of denying access may be warranted. Where safety or health hazards or liability issues press for complete closure of mines used as roosts, then physically denying access may also be warranted, but likely will not benefit the bats using the mine. A compromise might consist of closing the entrance with a bat-friendly gating.

Gating to protect roosts: Gating serves two general purposes: it protects internal resources from disturbance, destruction, or removal and it protects the public from dangers inherent in subterranean exploration. The latter purpose is especially relevant at abandoned mine sites, which, because they are more susceptible to subsidence and collapse than naturally occurring formations, represent liabilities to the landowner(s).

The popularity of gating as a means of closing mines has increased as the needs and plight of bats have become more topical, and there are many gating success stories (Kennedy 1999, Navo and Krabacher 2005). While the conservation benefits to bats of gating rather than backfilling are obvious, managers must be aware of the costs as well. In short, gates may be a more costly closure method than simply blasting or backfilling an entrance (although this is not always true; Tuttle and Taylor 1998). Gates require long-term monitoring and maintenance, and a poorly designed or constructed gate may alter internal conditions (e.g., airflow and temperature) and may thus result in harm to the colony it was meant to protect (Richter et al. 1993). There may be regulatory issues to consider as well since projects on federal land must comply with National Environmental Policy Act (NEPA) regulations and perhaps other state or local laws (Nieland and Meier 2002).

Design considerations: Gate designs and construction materials vary considerably. It is beyond the scope of this document to discuss details of all designs, or to describe how to build a gate. Readers interested in specific information on this topic are directed to several excellent resources (listed below), and they are encouraged to consult local or national experts and others with experience in cave and mine gating. However, a few general considerations are worth including here.

Pre-construction considerations: Gating requires planning and may be costly and time consuming. Various federal, state, and local agency regulations may need to be considered prior to project implementation. Not all caves or mines will warrant installation of gates, and availability of resources will likely limit the number of gating projects that can be completed. Therefore, it is important to prioritize sites during the planning process. When assigning priorities for gating projects, the following questions (adapted from Brown and Berry 2002) should be considered:

- **Does the roost harbor Threatened or Endangered species, or a species of management concern?** Such roosts should receive high conservation priority.
- **Is the roost a "significant" cave (FRCPA 1988)?** Federal law requires protection of such caves. In some (but not all) cases, protection may require gating.
- **Does the roost contain a maternity or hibernation colony of any bat species?** Such colonies are prone to disturbance-related abandonment and associated mortality and may benefit from the installation of a gate.
- **Does the roost shelter a large number of bats at any season?** Structures with large numbers of bats (e.g., more than 100) should be considered significant roosts and given high priority for gating or other protections. Determination of the size of colony that may be considered “large” will be case-specific. In general, colonies are smaller in the West than in the East.
- **Is the site internally complex with potential for different temperature regimes that may be necessary for bats at different seasons (especially if only a single survey was conducted)?** This is especially important if surveys at a site were limited. That is, a single visit during a single season may not yield bats, but if a site offers a particularly good microclimate for a particular life-stage, then it may receive use at other times of the year.
- **Is there potential for long-term stability of this site?**
- **Are other roosts available in the immediate vicinity for this species?** If alternate sites harbor bats but are subject to disturbance, then gating may provide valuable refuge for the bats.
Other considerations during pre-construction might include whether gating will attract the attention of passers-by. In some cases, roost entries are well hidden by vegetation, topography, or other obstructions, and they may receive little human disturbance as a result (Olson 2002). If gating is likely to increase the occurrence of humans at the entrance (and possibly result in vandalism), then gating may not be the best option. In such cases, re-routing of trails or roads (if they pass near the roost) may be a more effective means of diverting people away from the roost.

**Airflow:** Airflow into and out of caves and mines occurs as a result of various geophysical processes and the particular arrangement of shafts and adits in a mine (Tuttle and Taylor 1998) or of passages in a cave (Roebuck et al. 1999). Airflow effectively regulates temperature inside a cave or mine through surface and subsurface exchange of warm or cold air. Hence, gates must be designed and installed to minimize any restriction of airflow into or out of a structure. Roebuck et al. (1999) provide some general considerations with regard to gates and airflow:

- every cave or mine gate will experience different airflows
- the best location of a cave or mine gate is where the airflow is very slow
- solidity ratio of gates (the proportion of the cross-sectional area available for airflow comprised of the gate) must be kept to a minimum to reduce loss of airflow
- there is less than 1 percent pressure loss for low velocity airflow for typical gate materials at solidity ratios of 60 percent or less.

Where gate design or placement alters airflow, temperature regimes may be affected such that internal conditions are no longer favorable to roosting bats. Appropriate gate designs and placement should be determined by consultation of appropriate references or with persons experienced in these matters.

**Timing:** To avoid disturbance, construction of gates should be scheduled to occur at times when bats are not using the structure. For maternity roosts, construction should not occur between April and October. At hibernacula, gate construction should not occur between November and April. However, the exact range of dates during which bats are using a particular roost will vary with location, elevation, and local conditions, and will need to be determined on a case by case basis.

**Post-construction considerations:** Land management agencies are responsible for the protection of caves and mines and their resources. Failure to do so may be viewed as negligent and may lead to injury or death. Gates are intended to protect humans from potentially dangerous caves and mines while also protecting sensitive, internal (e.g., biological) resources. However, gates do not last forever. Attachment anchors loosen, and natural processes may degrade or compromise the integrity of the gate. Thus, gates must be monitored on a regular basis and repaired or replaced as necessary.

As with other structures on public land, gates may invite vandalism. Vandals may damage or dig under gates in attempts to gain entry. Regular long-term monitoring of gates should be used to identify and document acts of vandalism. Vandalism may be deterred through a combination of public education, improved gate design, and successful prosecution of vandals. Public education may involve, minimally, informational brochures and/or signs at trailheads or cave entrances explaining the reasons for the closure or restricted access and the penalties for unauthorized entry. Some agencies take education a step further and solicit involvement of recreational users (i.e., local caving groups) or public comment on the proposed gating project before construction begins. Vandalism may be prosecuted under any of several existing laws used for the protection of subterranean resources (reviewed above), and prosecution can be an effective deterrent to further acts of vandalism (Nieland and Meier 2002).

It is also important to conduct post-construction surveys to ensure that bats have continued to use the roosts. If bats are confirmed to have abandoned a roost, it may be a result of changes in internal conditions brought about by gating. In such cases, the gate may need to be modified or replaced.

**Management activities around roosts:** Management activities such as burning, timber harvest, road construction, vegetation alteration, and pesticide application in the vicinity of maternity or hibernation roosts should be conducted to minimize the level of disturbance and risk of direct impact to the colony. In general, if these activities must occur, they should be scheduled during times when bats are not present in the roost. Suggested buffer sizes for various management activities near roosts range from 150 to 500 feet for timber harvest, 250 feet for clear-cutting, and 2 miles...
for pesticide spraying (Pierson et al. 1999, Ellison et al. 2003a). Burning of vegetation near roosts has the potential to disrupt roosting bats if smoke is drawn into roosts. In addition, burning may alter the utility of foraging sites.

**Foraging habitat**: Adequate foraging sites should be maintained in close proximity (<5 miles) to roosting sites to minimize commuting costs. Ideally, foraging sites should contain a mosaic of vegetation types and seral stages to enhance the abundance of insect prey. *Corynorhinus townsendii* may use edge habitat and linear landscape elements (e.g., riparian zones) heavily, and alteration of these components should be avoided. Pierson et al. (1999) recommend that not more than half of the forested habitat within 0.5 miles of roosts be subjected to controlled burns per decade, and that no prescribed burning or vegetation alteration of shrub-steppe or pinyon-juniper habitat occur within 1.5 miles of roosts, and then only when bats are not present in the roost.

**Captive propagation and reintroduction**

To our knowledge, no propagation programs exist or are planned for this species. Given the current population status of *Corynorhinus 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 become necessary, then the success of these efforts would be questionable without substantial further research. Although many species of bats have been kept in captivity for the purpose of research (Wilson 1988), *C. townsendii* 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**

It is clear that we have learned much about the distribution and habits of bats over the past few decades. No doubt, this has resulted in part because of advancements in technology (e.g., bat-detectors and micro-radiotransmitters) that have allowed workers to address questions in new ways. It should be equally clear that we are still in the process of collecting even the most basic information on many species. For instance, *Corynorhinus townsendii* has only recently been confirmed at several locales in Nevada (Ports and Bradley 1996). As another example, a recent survey for bats in caves in Colorado (Siemers 2002) showed that 75 percent of the caves (8/12) that held Townsend’s big-eared bat were not previously known to be used by the bat.

Given the general lack of knowledge about roost sites for *Corynorhinus townsendii* in Region 2 and elsewhere, the information generated by the research presented above is exceptionally valuable for conservation of the species. Further, these examples illustrate an important message, namely that given our current state of understanding with regard to the local distribution of Townsend’s big-eared bats, substantial gains may be realized from modest effort.

We have only just begun to understand, in many places, where bats occur and how many there are, and we have only a notion about the complex ways in which many species of bats interact with the physical environment and how they are likely to respond when humans alter that environment. This is particularly so for cryptic species such as *Corynorhinus townsendii*. Thus, efforts to survey known and suspected habitat regularly for the presence of *C. townsendii* may be nearly as important as protecting known roosts. Although protection of known roosts should be considered a higher priority given the status of *C. townsendii*, the two efforts build upon and complement one another.

Given limitations in our knowledge of population size, patterns of movement, foraging ecology, and extrinsic factors affecting demographics, Pierson et al. (1999) identified four research goals to fill gaps in our understanding and to inform management decisions regarding *Corynorhinus townsendii*:

- assess the degree of variability in roosts throughout the species’ range
- evaluate roost microclimate and structural parameters for predictive screening and site evaluation
- 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
- examine the direct and indirect impacts of environmental toxicants, particularly pesticides, on populations.
We would add to this list:

- develop baseline estimates of abundance and population
- develop a better estimate of current population trends
- identify key roosting habitat, particularly hibernacula and maternity colonies
- gain a more thorough understanding of metapopulation dynamics.

It is only through evaluation of population trends, which necessitates reliable baseline population estimates for comparison, that we will know if management efforts are having desired effects. Population trends, in turn, rely on basic knowledge of abundance and density from season to season. Although the logistical hurdles to such an endeavor are not trivial, advancements in technology combined with dedicated management direction and updated evaluation approaches should make this goal more tenable.

The authors find the last item on the above list particularly interesting. *Corynorhinus townsendii* likely faces significant hurdles to recolonization of unoccupied habitat (e.g., low dispersal, specific habitat requirements, and high habitat fragmentation), but no studies have investigated whether colonies are truly isolated or exist in a metapopulation structure. The presence and extent of *C. townsendii* metapopulation(s) could have important implications for conservation of the species, because without such inter-population dynamics, it could be difficult (if not impossible) for areas that have lost populations through extinction to be naturally recolonized.
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Schmidly, D.J. 1991. The bats of Texas. Texas A & M University Press, College Station, TX.


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SELECT REFERENCES FOR SPECIFIC TOPICS

Townsend’s Big-Eared Bat Conservation Plans/Assessments

Western Populations


Eastern Populations


Western Bat Conservation Plans by State

Arizona


Colorado


Nevada


South Dakota


General Methods/Considerations for Surveying and Monitoring Bats


Survey, Management and Protection of Bats in Caves and Mines


**General References to Caves in USDA Forest Service Region 2**


**General References About Bats in USDA Forest Service Region 2**


Jones, J.K., Jr. 1964. Distribution and taxonomy of mammals of Nebraska. University of Kansas Press, Lawrence, KS.


Ulrich, T. 1986. Mammals of the Northern Rockies. Mountain Press, Missoula, MT.

**General Bat Biology, Ecology, and Distribution**


**APPENDIX A**

**Explanation of Ranking Codes and Management Status Abbreviations**

Table A1a. Wyoming Game and Fish Department status rankings. 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. Seven classes of Native Status Species (NSS) are recognized, of which classes 1, 2, 3 and 4 are considered to be high priorities for conservation attention (Wyoming Game and Fish Department 2005).

<table>
<thead>
<tr>
<th>Rank</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>NSS1</td>
<td>Includes species with populations that are greatly restricted or declining (extirpation appears possible) and with ongoing significant loss of habitat.</td>
</tr>
<tr>
<td>NSS2</td>
<td>Species in which: (1) habitat is restricted or vulnerable (but no recent or significant loss has occurred) and populations are greatly restricted or declining (extirpation appears possible); or (2) species with ongoing significant loss of habitat and populations that are declining or restricted in numbers and distribution (extirpation is possible but not imminent).</td>
</tr>
<tr>
<td>NSS3</td>
<td>Species in which: (1) habitat is vulnerable to loss, but not restricted; populations are greatly restricted or declining (extirpation appears possible); species is not sensitive to human disturbance; 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.</td>
</tr>
</tbody>
</table>

NSS = Native Species Status


<table>
<thead>
<tr>
<th>Rank</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>GX</td>
<td>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.</td>
</tr>
<tr>
<td>GH</td>
<td>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).</td>
</tr>
<tr>
<td>G1</td>
<td>Critically Imperilled – Critically imperilled 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 (&lt;1,000) or acres (&lt;2,000) or linear miles (&lt;10).</td>
</tr>
<tr>
<td>G2</td>
<td>Imperilled – Imperilled 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).</td>
</tr>
<tr>
<td>G3</td>
<td>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.</td>
</tr>
<tr>
<td>G4</td>
<td>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.</td>
</tr>
<tr>
<td>G5</td>
<td>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.</td>
</tr>
</tbody>
</table>

**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. |
| HYB  | 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.) |
**Table A1b (concluded).**

<table>
<thead>
<tr>
<th>Rank</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>?</td>
<td>Inexact Numeric Rank – Denotes inexact numeric rank</td>
</tr>
<tr>
<td>Q</td>
<td>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.</td>
</tr>
<tr>
<td>C</td>
<td>Captive or Cultivated Only – Taxon at present is extant only in captivity or cultivation, or as a reintroduced population not yet established.</td>
</tr>
</tbody>
</table>

**Infraspecific Taxon Ranks**

| T# | 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 imperilled 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 A1c. National (N) and Subnational1 (S) Heritage Status rank definitions.**

<table>
<thead>
<tr>
<th>Rank</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>NX</td>
<td>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.</td>
</tr>
<tr>
<td>SX</td>
<td>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.</td>
</tr>
<tr>
<td>NH</td>
<td>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 (&lt;1,000).</td>
</tr>
<tr>
<td>SH</td>
<td>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).</td>
</tr>
<tr>
<td>N1</td>
<td>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.</td>
</tr>
<tr>
<td>N2</td>
<td>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.</td>
</tr>
<tr>
<td>N3</td>
<td>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.</td>
</tr>
<tr>
<td>N4</td>
<td>Unranked – Nation or subnation* rank not yet assessed.</td>
</tr>
<tr>
<td>NE</td>
<td>Unrankable – Currently unrankable due to lack of information or due to substantially conflicting information about status or trends.</td>
</tr>
<tr>
<td>NE#</td>
<td>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).</td>
</tr>
<tr>
<td>HYB</td>
<td>Hybrid – Element not ranked because it represents an interspecific hybrid, not a species.</td>
</tr>
<tr>
<td>NE</td>
<td>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.).</td>
</tr>
<tr>
<td>SA</td>
<td>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.</td>
</tr>
<tr>
<td>NZ</td>
<td>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.</td>
</tr>
<tr>
<td>NP</td>
<td>Potential – Potential that element occurs in the nation or subnation* but no extant or historic occurrences are accepted.</td>
</tr>
</tbody>
</table>
**Table A1c (concluded).**

<table>
<thead>
<tr>
<th>Rank</th>
<th>Definition</th>
</tr>
</thead>
<tbody>
<tr>
<td>NR</td>
<td><strong>Reported</strong> – 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.</td>
</tr>
<tr>
<td>SR</td>
<td><strong>Reported</strong> – 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.</td>
</tr>
<tr>
<td>NSYN</td>
<td><strong>Synonym</strong> – 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.</td>
</tr>
<tr>
<td>SSYN</td>
<td><em>N or S rank has been assigned and is under review. Contact the individual subnational</em> Natural Heritage program for assigned rank.</td>
</tr>
<tr>
<td>Not provided</td>
<td>Species is known to occur in this nation or subnation.* Contact the individual subnational* Natural Heritage program for assigned rank.</td>
</tr>
</tbody>
</table>

**Breeding Status Qualifiers**

| B   | **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 Qualifiers**

| ?   | **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. |

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

Detailed Discussion of Life History Model

A life history model was developed for this Species Assessment by D. McDonald and T. Ise. We summarized the main points of their discussion in the body of the assessment. Here we provide the full discussion for readers interested in the complexities of the analysis.

Life cycle graph and model development

The life history described by Knox (1983) provided the basis for a life cycle graph (Figure B1) and a matrix population analysis with a post-breeding census (Cochran and Ellner 1992, McDonald and Caswell 1993, Caswell 2000) for Townsend’s big-eared bat. The model has three kinds of input terms: \( P_i \) describing survival rates, \( m_i \) describing fertilities, and \( B_i \) describing probability of reproduction (Table B1). Table B2a shows the symbolic terms in the projection matrix corresponding to the life cycle graph. Table B2b gives the corresponding numeric values. The model assumes female demographic dominance so that, for example, fertilities are given as female offspring per female. The population growth rate (\( \lambda \)) is 1.000 based on the estimated vital rates used for the matrix. Although this suggests a stationary population, the value is subject to the many assumptions used to derive the transitions and should not be interpreted as an indication of the general well-being and stability of the population. Other parts of the analysis provide a better guide for assessment.

Sensitivity analysis

A useful indication of the state of the population comes from the sensitivity and elasticity analyses. Sensitivity is the effect on \( \lambda \) of an absolute change in the vital rates (\( a_{ij} \), the arcs in the life cycle graph (Figure B1) and the cells in the matrix, A [Table B2]). Sensitivity analysis provides several kinds of useful information (see Caswell 1989, p.118-119). First, sensitivities show “how important” a given vital rate is to \( \lambda \) or fitness. For example, one can use sensitivities to assess the relative importance of survival (\( P_i \)) and reproductive (\( F_i \)) transitions. Second, sensitivities can be used to evaluate the effects of inaccurate estimation of vital rates from field studies. Inaccuracy will usually be due to paucity of data, but it could also result from use of inappropriate estimation techniques or other errors of analysis. In order to improve the accuracy of the models, researchers should concentrate additional effort on transitions with large sensitivities. Third, sensitivities can quantify the effects of environmental perturbations, wherever those can be linked to effects on stage-specific survival or fertility rates. Fourth, managers can concentrate on the most important transitions. For example, they can assess which stages or vital rates are most critical to increasing \( \lambda \) of endangered species or the “weak links” in the life cycle of a pest. Table B3 shows the “possible sensitivities only” matrix for this analysis (one can calculate sensitivities for non-existent transitions, but these are usually either meaningless or biologically impossible – for example, the sensitivity of \( \lambda \) to moving from Age Class 3 to Age Class 2).

\begin{figure}[h]
  \centering
  \includegraphics[width=\textwidth]{life_cycle_graph.png}
  \caption{Age-classified life cycle graph for Townsend’s big-eared bat. The numbered circles (nodes) represent the six age classes. The arrows (arcs) connecting the nodes represent the vital rates – transitions between age classes such as survival (\( P_{21} \)) or fertility (the arcs pointing back toward the first node from Nodes 1 through 5). Note that reproduction begins at the end of the first year, and that the reproductive arcs include terms for survival of female parent (\( P_i \)) as well as number of female offspring per female (\( m_i \)).}
\end{figure}
In general, changes that affect one type of age class or stage will also affect all similar age-classes or stages. For example, any factor that changes the annual survival rate of Age Class 2 females is very likely to cause similar changes in the survival rates of other “adult” reproductive females (those in Age Classes 3 through 5). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the summed sensitivity of $\lambda$ to changes in the fertilities

<p>| Table B1. Parameter values for the component terms ($P_i$, $m_i$, and $B_i$) that make up the vital rates in the projection matrix for Townsend’s big-eared bats. |</p>
<table>
<thead>
<tr>
<th>Parameter</th>
<th>Numeric value</th>
<th>Interpretation</th>
</tr>
</thead>
<tbody>
<tr>
<td>$m$</td>
<td>0.5</td>
<td>Number of female offspring produced by a female</td>
</tr>
<tr>
<td>$B_1$</td>
<td>0.9</td>
<td>Probability of reproduction of Age Class 1</td>
</tr>
<tr>
<td>$B_a$</td>
<td>0.95</td>
<td>Probability of reproduction of Age Class 2 to 5 (adult females)</td>
</tr>
<tr>
<td>$P_{21}$</td>
<td>0.576</td>
<td>First-year survival rate</td>
</tr>
<tr>
<td>$P_a$</td>
<td>0.85</td>
<td>Annual survival rate of adults</td>
</tr>
</tbody>
</table>

<p>| Table B2a. Symbolic values. |</p>
<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>$P_{21}mB_1$</td>
<td>$P_mB_a$</td>
<td>$P_mB_a$</td>
<td>$P_mB_a$</td>
<td>$P_mB_a$</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>$P_{21}$</td>
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</tr>
<tr>
<td>3</td>
<td>$P_a$</td>
<td></td>
<td></td>
<td></td>
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</tr>
<tr>
<td>4</td>
<td>$P_a$</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>$P_a$</td>
<td></td>
<td></td>
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<td></td>
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</tr>
<tr>
<td>6</td>
<td>$P_a$</td>
<td></td>
<td></td>
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<td></td>
</tr>
</tbody>
</table>

<p>| Table B2b. Numeric values. |</p>
<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.259</td>
<td>0.4038</td>
<td>0.4038</td>
<td>0.4038</td>
<td>0.4038</td>
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<tr>
<td>2</td>
<td>0.576</td>
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<tr>
<td>3</td>
<td>0.85</td>
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<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0.85</td>
<td></td>
<td></td>
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<tr>
<td>5</td>
<td>0.85</td>
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<td></td>
</tr>
<tr>
<td>6</td>
<td>0.85</td>
<td></td>
<td></td>
<td></td>
<td></td>
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</tr>
</tbody>
</table>

| Table B2. The input matrix of vital rates, $A$ (with cells $a_{ij}$) corresponding to the Townsend’s big-eared bat life cycle graph (Figure B1). The first row of the matrix contains values associated with reproductive output for a given stage class. Values in the other rows represent the probabilities of an individual moving from one stage to the next. |

<p>| Table B3. Possible sensitivities only matrix, $S_p$ (blank cells correspond to zeros in the original matrix, $A$). The three transitions to which the $\lambda$ of Townsend’s big-eared bats is most sensitive are highlighted: first-year survival ($s_{21} = 0.476$), first-year reproduction ($s_{11} = 0.370$), and survival of Age Class 2 ($s_{12} = 0.221$). |</p>
<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.370</td>
<td>0.213</td>
<td>0.181</td>
<td>0.154</td>
<td>0.131</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.476</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td>0.221</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>4</td>
<td>0.135</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td>0.062</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td>0.000</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

In general, changes that affect one type of age class or stage will also affect all similar age-classes or stages. For example, any factor that changes the annual survival rate of Age Class 2 females is very likely to cause similar changes in the survival rates of other “adult” reproductive females (those in Age Classes 3 through 5). Therefore, it is usually appropriate to assess the summed sensitivities for similar sets of transitions (vital rates). For this model, the result is that the summed sensitivity of $\lambda$ to changes in the fertilities...
is important. Townsend’s big-eared bat shows large sensitivity (1.049; 54 percent of total) to changes in fertility (the first row of the matrix in Table B3). First-year survival is 0.476 (24 percent of total), and the summed “reproductive” survival sensitivity is 0.418 (22 percent of total). The major conclusion from the sensitivity analysis is that both survival and fertility are important to population viability.

Elasticity analysis

Elasticities have the useful property of summing to 1.0 and are useful in resolving a problem of scale that can affect conclusions drawn from the sensitivities. Interpreting sensitivities can be somewhat misleading because survival rates and reproductive rates are measured on different scales. For instance, a change of 0.5 in survival may be a big alteration (e.g., a change from a survival rate of 90 to 40 percent). On the other hand, a change of 0.5 in fertility may be a very small proportional alteration (e.g., a change from a clutch of 3,000 eggs to 2,999.5 eggs). Therefore, because elasticities are the sensitivities of \( \lambda \) to proportional changes in the vital rates \( (a_{ij}) \), the problem of differences in units of measurement is largely avoided. The difference between conclusions based on analyses of sensitivity versus elasticity results from the weighting of the elasticities by the value of the original arc coefficients (the \( a_{ij} \) cells of the projection matrix). Management conclusions will depend on whether changes in vital rates are likely to be absolute (guided by sensitivities) or proportional (guided by elasticities). By using elasticities, one can further assess key life history transitions and stages as well as the relative importance of reproduction \( (F) \) and survival \( (P) \) for a given species.

Elasticities for Townsend’s big-eared bats are shown in Table B4. The \( \lambda \) of Townsend’s big-eared bats is most elastic to changes in first-year survival (\( e_{21} = 0.274 \)), followed by the survival of females at Age Class 2 (\( e_{32} = 0.188 \)) and survival of Age Class 3 (\( e_{43} = 0.115 \)). Note the considerably lower relative importance of fertility transitions in the elasticity analysis relative to the sensitivity analysis.

### Table B4

<table>
<thead>
<tr>
<th>Stage</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>0.096</td>
<td>0.086</td>
<td>0.073</td>
<td>0.062</td>
<td>0.053</td>
<td></td>
</tr>
<tr>
<td>2</td>
<td>0.274</td>
<td></td>
<td>0.188</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>3</td>
<td></td>
<td>0.115</td>
<td></td>
<td>0.053</td>
<td></td>
<td>0.000</td>
</tr>
<tr>
<td>4</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>5</td>
<td></td>
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<td></td>
<td></td>
</tr>
<tr>
<td>6</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
eared bats are most susceptible to habitat degradation that affects reproduction.

Other demographic parameters

The stable (st)age distribution (SAD; Table B5) describes the proportion of each Stage (or age class) in a population at demographic equilibrium. Under a deterministic model, any unchanging matrix will converge on a population structure that follows the stable age distribution, regardless of whether the population is declining, stationary or increasing. Under most conditions, populations not at equilibrium will converge to the SAD within 20 to 100 census intervals. For Townsend’s big-eared bat at the time of the post-breeding annual census (just after the end of the breeding season), newborns represent 32 percent of the population, and the remaining 68 percent consists of adult stages. Reproductive values (Table B6) can be thought of as describing the “value” of a stage as a seed for population growth relative to that of the first (newborn or, in this case, egg) stage. The reproductive value of the first stage is always 1.0. A female individual in Age Class 2 is “worth” 1.3 female newborns, and so on (Caswell 2001). The reproductive value is calculated as a weighted sum of the present and future reproductive output of a stage discounted by the probability of surviving (Williams 1966). The peak reproductive value (1.3) occurs at the second age class, and these females are the most important stage in the life cycle. The relatively small difference between newborn and peak reproductive value (1.3; cf. peak of 2,470 in plains leopard frog) reflects both a fairly even distribution of sensitivity and elasticity values across the life cycle and the high survival rate of first-year individuals relative to adults (an increase of only 48 percent vs. an increase of 1,056 percent in the plains leopard frog). The cohort generation time for the bat is 2.7 years (SD = 1.4 years).

Stochastic model

We conducted a stochastic matrix analysis for Townsend’s big-eared bats. We incorporated stochasticity in several ways, by varying different combinations of vital rates or by varying the amount of stochastic fluctuation (Table B7). Under Variant 1 we subjected first-year survival ($P_{21}$) to stochastic fluctuations. Under Variant 2 we varied the survival of all age classes, $P_i$. Because of the small, invariant litter size, we did not model stochastic variation in the fertilities. Each run consisted of 2,000 census intervals (years) beginning with a population size of 10,000 distributed according to the Stable Age Distribution (SAD) under the

Table B5. Stable age distribution (right eigenvector) for female Townsend’s big-eared bats. At the census, 32 percent of the individuals in the population should be newborns. The remaining 68 percent of individuals will be reproductive adults.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Description</th>
<th>Proportion</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Female newborns ($F_i = 0.2592$)</td>
<td>0.319</td>
</tr>
<tr>
<td>2</td>
<td>Adult females ($F_i = 0.40375$)</td>
<td>0.184</td>
</tr>
<tr>
<td>3</td>
<td>&quot;</td>
<td>0.156</td>
</tr>
<tr>
<td>4</td>
<td>&quot;</td>
<td>0.133</td>
</tr>
<tr>
<td>5</td>
<td>&quot;</td>
<td>0.113</td>
</tr>
<tr>
<td>6</td>
<td>Maximum Age Class</td>
<td>0.096</td>
</tr>
</tbody>
</table>

Table B6. Reproductive values for female Townsend’s big-eared bats. Reproductive values can be thought of as describing the “value” of an age class as a seed for population growth relative to that of the first (newborn or, in this case, egg) age class. The reproductive value of the first age class is always 1.0. The relatively low peak reproductive value is highlighted.

<table>
<thead>
<tr>
<th>Age Class</th>
<th>Description</th>
<th>Reproductive values</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>Female newborns ($F_i = 0.2592$)</td>
<td>1.00</td>
</tr>
<tr>
<td>2</td>
<td>Adult females ($F_i = 0.40375$)</td>
<td>1.29</td>
</tr>
<tr>
<td>3</td>
<td>&quot;</td>
<td>1.04</td>
</tr>
<tr>
<td>4</td>
<td>&quot;</td>
<td>0.75</td>
</tr>
<tr>
<td>5</td>
<td>&quot;</td>
<td>0.40</td>
</tr>
<tr>
<td>6</td>
<td>Maximum Age Class</td>
<td>0.00</td>
</tr>
</tbody>
</table>
deterministic model. Beginning at the SAD helps avoid the effects of transient, non-equilibrium dynamics. The overall simulation consisted of 100 runs (each with 2,000 cycles). We varied the amount of fluctuation by changing the standard deviation of the random normal distribution from which the stochastic vital rates were selected. The default value was a standard deviation of one quarter of the “mean” (with this “mean” set at the value of the original matrix entry \( a_{ij} \) under the deterministic analysis). Variant 3 affected the same transition as Variant 2 \((P_i)\) but was subjected to slightly larger variation (SD was 1 / 3.5 [= 0.286 compared to 0.25] of the mean). We calculated the stochastic growth rate, log\(\lambda \), according to Equation 14.61 of Caswell (2000), after discarding the first 1,000 cycles in order to further avoid transient dynamics.

The stochastic model (Table B7) produced two major results. First, altering the survival rates had a somewhat greater effect on \( \lambda \) than did altering all the fertilities. For example, the median ending size under the varying survival of newborns under Variant 1 was 299.2 from the starting size of 10,000. In contrast, varying the survival rates of all age classes under Variant 2 resulted in a further decline of median size to 134.1. This difference in the effects of stochastic variation is predictable largely from the elasticities. \( \lambda \) was more elastic to changes in survival, \( P_i \) than it was to changes in the fertilities. Second, large-effect stochasticity has a negative effect on population dynamics. This negative effect occurs despite the fact that the average vital rates remain the same as under the deterministic model – the random selections are from a symmetrical distribution. This apparent paradox is due to the lognormal distribution of stochastic ending population sizes (Caswell 2000). The lognormal distribution has the property that the mean exceeds the median, which exceeds the mode. Any particular realization will therefore be most likely to end at a population size considerably lower than the initial population size. For Townsend’s big-eared bats under the survival Variant 2, 66 out of 100 trials of stochastic projection went to extinction vs. 20 under the fertilities Variant 1. Variant 3 shows that the magnitude of fluctuation has a potentially large impact on the detrimental effects of stochasticity. Increasing the magnitude of fluctuation also increased the severity of the negative impacts – the number of extinctions went from 66 in Variant 2 to 82 in Variant 3 when the magnitude of fluctuation was slightly amplified. These results suggest that populations of Townsend’s big-eared bats are vulnerable both to stochastic fluctuations in production of newborns (due, for example, to annual climatic change or to human disturbance) and to variations in survival. In contrast to some other life cycles, the relative impacts of stochasticity in fertility and survival are fairly evenly balanced (cf. Blanding’s turtle assessment, where survival effects are dramatically more important than are fertility effects). Pfister (1998) showed that for a wide range of empirical life histories, high sensitivity or elasticity was negatively correlated with high rates of temporal variation. That is, most species appear to have responded to strong selection by having low variability for sensitive transitions in their life cycles. A possible concern is that anthropogenic impacts may induce variation in previously invariant vital rates (such as annual adult survival), with consequent detrimental effects on population dynamics. For the bats, with

<table>
<thead>
<tr>
<th>Input factors:</th>
<th>Variant 1</th>
<th>Variant 2</th>
<th>Variant 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Affected cells ( P_i )</td>
<td>1.00010</td>
<td>1.00010</td>
<td>1.00010</td>
</tr>
<tr>
<td>S.D. of random normal distribution</td>
<td>1/4</td>
<td>1/4</td>
<td>1/3.5</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Output values:</th>
<th>Variant 1</th>
<th>Variant 2</th>
<th>Variant 3</th>
</tr>
</thead>
<tbody>
<tr>
<td>Deterministic ( \lambda )</td>
<td>1.00010</td>
<td>1.00010</td>
<td>1.00010</td>
</tr>
<tr>
<td># Extinctions / 100 trials</td>
<td>20</td>
<td>66</td>
<td>82</td>
</tr>
<tr>
<td>Mean extinction time</td>
<td>1,657.4</td>
<td>1,344.2</td>
<td>1,135.3</td>
</tr>
<tr>
<td># Declines / # survived pop</td>
<td>73/80</td>
<td>31/34</td>
<td>18/18</td>
</tr>
<tr>
<td>Mean ending population size</td>
<td>8,254.5</td>
<td>2,166.2</td>
<td>365.0</td>
</tr>
<tr>
<td>Standard deviation</td>
<td>41,190.3</td>
<td>5,895.7</td>
<td>865.2</td>
</tr>
<tr>
<td>Median ending population size</td>
<td>299.16</td>
<td>134.11</td>
<td>49.93</td>
</tr>
<tr>
<td>Log ( \lambda_s )</td>
<td>-0.00269</td>
<td>-0.00548</td>
<td>-0.00766</td>
</tr>
<tr>
<td>( \lambda_s )</td>
<td>0.9973</td>
<td>0.9945</td>
<td>0.9924</td>
</tr>
<tr>
<td>% reduction in ( \lambda )</td>
<td>0.279</td>
<td>0.557</td>
<td>0.773</td>
</tr>
</tbody>
</table>

Table B7. Summary of three variants of a stochastic projection for Townsend’s big-eared bats.
a relatively even balance between the impacts due to fertility and survival changes, and with the small invariant litter size, the life history may not allow the kind of adjustment of risk load that may be possible in other species.

Potential refinements of the models

Clearly, the better the data on survival rates, the more accurate the resulting analysis. Data from natural populations on the range of variability in the vital rates would allow more realistic functions to model stochastic fluctuations. For example, time series based on actual temporal or spatial variability, would allow construction of a series of “stochastic” matrices that mirrored actual variation. One advantage of such a series would be the incorporation of observed correlations between variation in vital rates. Where we varied $F_i$ and $P_i$ values simultaneously, we assumed that the variation was uncorrelated, based on the assumption that factors affecting reproduction and, for example, overwinter survival would occur at different seasons or be due to different and likely uncorrelated factors (e.g., predation load vs. climatic severity or water levels). Using observed correlations would improve on this assumption by incorporating forces that we did not consider. Those forces may drive greater positive or negative correlation among life history traits. Other potential refinements include incorporating density-dependent effects. At present, the data appear insufficient to assess reasonable functions governing density dependence.


References


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