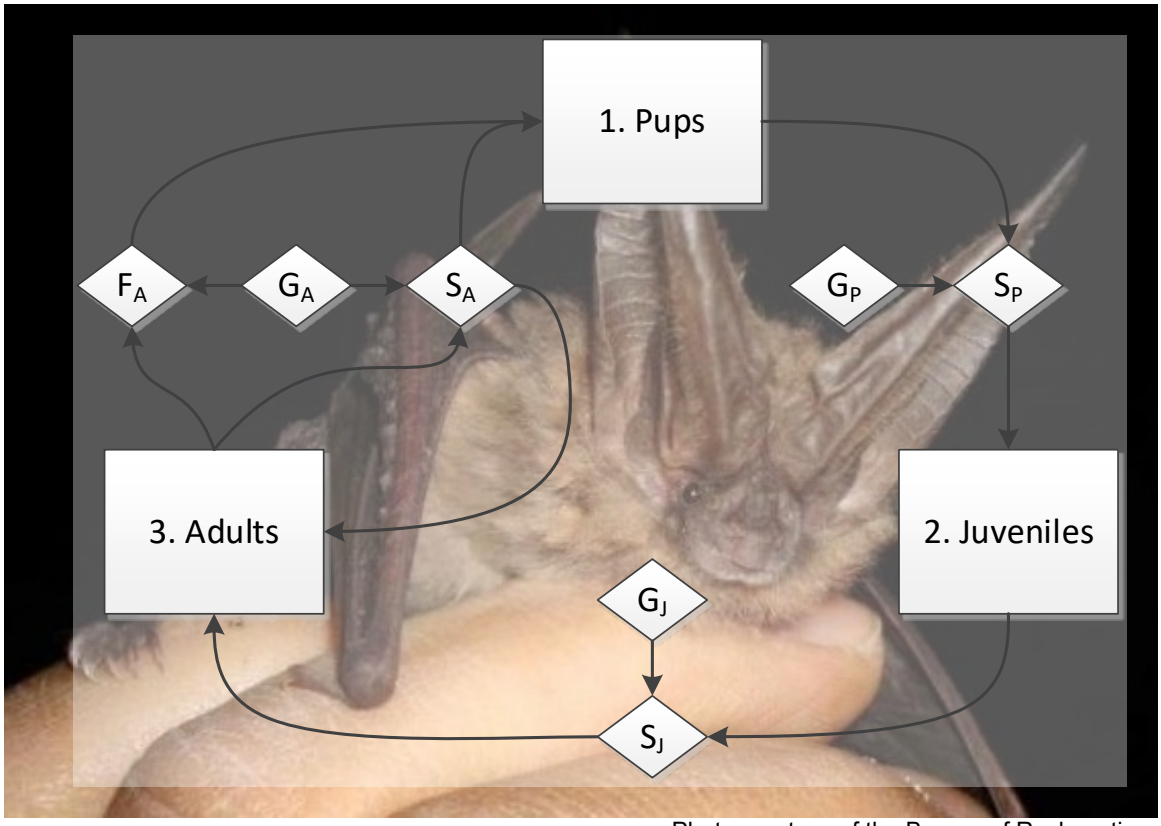
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Townsend's Big-eared Bat (*Corynorhinus townsendii*) (PTBB) Basic Conceptual Ecological Model for the Lower Colorado River



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Work conducted under LCR MSCP Work Task G6

April 2020

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Lower Colorado River Multi-Species Conservation Program

Townsend's Big-eared Bat (*Corynorhinus townsendii*) (PTBB) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

aka	also know as
AZGFD	Arizona Game and Fish Department
CEM	conceptual ecological model
cm	centimeter(s)
CRIT	Colorado River Indian Tribes
CRTR	Colorado River Terrestrial and Riparian
DNA	deoxyribonucleic acid
ERP	Sacramento-San Joaquin Delta Ecosystem Restoration Program
ft	foot/feet
HCP	Habitat Conservation Plan
km	kilometer(s)
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
mm	millimeter(s)
PTBB	Townsend's big-eared bat (*Corynorhinus townsendii*); formerly referred more narrowly to the subspecies, the pale Townsend's big-eared bat (*C. t. pallescens*)
Reclamation	Bureau of Reclamation

Symbols

°C	degrees Celsius
°F	degrees Fahrenheit
≥	greater than or equal to
<	less than

Definitions

For the purposes of this document, vegetation layers are defined as follows:

Canopy – The canopy is the uppermost strata within a plant community. The canopy is exposed to the sun and captures the majority of its radiant energy.

Understory – The understory comprises plant life growing beneath the canopy without penetrating it to any extent. The understory exists in the shade of the canopy and usually has lower light and higher humidity levels. The understory includes subcanopy trees and the shrub and herbaceous layers.

Shrub layer – The shrub layer is comprised of woody plants between 0.5 and 2.0 meters in height.

Herbaceous layer – The herbaceous layer is most commonly defined as the forest stratum composed of all vascular species that are 0.5 meter or less in height.

CONTENTS

Page

Foreword ..... **v**

Executive Summary **ES-1**
Conceptual Ecological Models ES-1
Conceptual Ecological Model Structure ES-3
Results ES-5

Chapter 1 – Introduction **1-1**
Townsend's Big-eared Bat Reproductive Ecology 1-3
Conceptual Ecological Model Purposes 1-7
Conceptual Ecological Model Structure 1-8

Chapter 2 – Townsend's Big-eared Bat Life-Stage Model **2-1**
Introduction to the Townsend's Big-eared Bat Life Cycle 2-1
Pups 2-3
Juveniles 2-3
Adults 2-4

Chapter 3 – Critical Biological Activities and Processes **3-1**
Breeding 3-2
Chemical Stress 3-3
Competition 3-4
Disease 3-5
Feeding 3-6
Foraging 3-6
Inter-Site Movement 3-9
Maternal Care 3-11
Mechanical Stress 3-12
Predation 3-13
Roosting: Cold Season, Warm Season, Interim 3-15
Roosting: Cold Season 3-15
Roosting: Warm Season 3-16
Roosting: Interim 3-17
Thermal Stress 3-18

Chapter 4 – Habitat Elements **4-1**
Anthropogenic Disturbance 4-2
Arthropod Community 4-3
Caves and Cave Analogs 4-4
Chemical Contaminants 4-7
Fire Regime 4-8
Infectious Agents 4-9

Page

Maternal Care 4-9
Monitoring, Capture, Handling 4-10
Temperature 4-11
Tree and Shrub Vegetation 4-13
Vertebrate Community 4-17
Water Availability 4-19

Chapter 5 – Controlling Factors 5-1
Conservation Monitoring and Research Programs 5-2
Fire Management 5-2
Habitat Development and Management 5-3
Mining and Mine Management 5-4
Nuisance Species Introduction and Management 5-5
Recreational Use of Caves and Abandoned Mines 5-6
Surrounding Land Use 5-6
Water Storage-Delivery System Design and Operation 5-7

Chapter 6 – Conceptual Ecological Model by Life Stage 6-1
Life Stage 1 – Pups 6-4
Life Stage 2 – Juveniles 6-9
Life Stage 3 – Adults 6-17

Chapter 7 – Causal Relationships Across All Life Stages 7-1
Causal Relationships Affecting Cold- and Warm-Season Roosting Habitat 7-2
Causal Relationships Affecting Foraging, Commuting, and Night-Roosting Habitat 7-5

Chapter 8 – Discussion and Conclusions 8-1

Literature Cited L-1

Acknowledgments A-1

Tables

Table Page

1 Proposed life stages and life-stage outcomes for Townsend's big-eared bats in the LCR ecosystem..... 2-1
2 Proposed critical biological activities and processes for Townsend's big-eared bats in the LCR ecosystem and their distribution among life stages 3-1
3 Proposed habitat elements for Townsend's big-eared bats in the LCR ecosystem and the critical biological activities and processes they may directly affect 4-1
4 Proposed controlling factors affecting Townsend's big-eared bats in the LCR ecosystem and the habitat elements they directly affect 5-1
5 Proposed magnitudes of causal relationships in the CEM for Townsend's big-eared bats in the LCR ecosystem 8-1
6 Proposed level of understanding of causal relationships in the CEM for Townsend's big-eared bats in the LCR ecosystem..... 8-1

Figures

Figure Page

1 Proposed life history model for the Townsend's big-eared bat. 2-2
2 Diagram conventions for LCR MSCP species conceptual ecological models..... 6-3
3 CEM master diagram for Townsend's big-eared bat life stage 1 – pup life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes. 6-7
4 CEM master diagram for Townsend's big-eared bat life stage 2 – juvenile life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes. 6-15
5 CEM master diagram for Townsend's big-eared bat life stage 3 – adult life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes. 6-25

Attachments

Attachment

1 Species Conceptual Ecological Model Methodology for the Lower Colorado River Multi-Species Conservation Program

Foreword

The Lower Colorado River Multi-Species Conservation Program (LCR MSCP) Habitat Conservation Plan requires the creation, and long-term stewardship, of habitat for 20 covered species. This is both an exciting and daunting challenge—exciting, in that success would mean a major conservation achievement in the lower Colorado River landscape, and daunting, in that we need to simultaneously manage our lands for the benefit of 20 species in a mosaic of land cover types. To do so, we need to develop a common understanding of the habitat requirements of each species and the stewardship required to meet those needs.

To provide a framework to capture and share the information that forms the foundation of this understanding, conceptual ecological models (CEMs) for each covered species have been created under the LCR MSCP's Adaptive Management Program. The LCR MSCP's conceptual ecological models are descriptions of the functional relationships among essential components of a species' life history, including its habitat, threats, and drivers. They tell the story of "what's important to the animal" and how our stewardship and restoration actions can change those processes or attributes for the betterment of their habitat. As such, CEMs can provide:

- A synthesis of the current understanding of how a species' habitat works. This synthesis can be based on the published literature, technical reports, or professional experience.

- Help in understanding and diagnosing underlying issues and identifying land management opportunities.

- A basis for isolating cause and effect and simplifying complex systems. These models also document the interaction among system drivers.

- A common (shared) framework or "mental picture" from which to develop management alternatives.

- A tool for making qualitative predictions of ecosystem responses to stewardship actions.

- A way to flag potential thresholds from which system responses may accelerate or follow potentially unexpected or divergent paths.

- A means by which to outline further restoration, research, and development and to assess different restoration scenarios.

- A means of identifying appropriate monitoring indicators and metrics.

- A basis for implementing adaptive management strategies.

Most natural resource managers rely heavily upon CEMs to guide their work, but few explicitly formulate and express the models so they can be shared, assessed, and improved. When this is done, these models provide broad utility for ecosystem restoration and adaptive management.

Model building consists of determining system parts, identifying the relationships that link these parts, specifying the mechanisms by which the parts interact, identifying missing information, and exploring the model's behavior (Heemskerk et al. 2003[1]). The model building process can be as informative as the model itself, as it reveals what is known and what is unknown about the connections and causalities in the systems under management.

It is important to note that CEMs are not meant to be used as prescriptive management tools but rather to give managers the information needed to help inform decisions. These models are conceptual and qualitative. They are not intended to provide precise, quantitative predictions; rather, they allow us to virtually "tweak the system" free of the constraints of time and cost to develop a prediction of how a system might respond over time to a variety of management options. For a single species, a documented model is a valuable tool, but for 20 species, they are imperative. For the successful management of multiple species in a world of competing interests (species versus species); potentially conflicting needs, goals, and objectives; long response times; and limited resources, these models can help land managers experiment from the safety of the desktop. Because quantitative data can be informative, habitat parameters that have been quantified in the literature are presented (attachment 2) in this document for reference purposes.

These models are intended to be "living" documents that should be updated and improved over time. The model presented here should not be viewed as a definitive monograph of a species' life history but rather as a framework for capturing the knowledge and experience of the LCR MSCP's scientists and land stewards. While ideally the most helpful land management tool would be a definitive list of do's and don'ts, with exact specifications regarding habitat requirements that would allow us to engineer exactly what the species we care about need to survive and thrive, this is clearly not possible. The fact is, that despite years of active management, observation, and academic research on many of the LCR MSCP species of concern, there may not be enough data to support developing such detailed, prescriptive land management.

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[1] Heemskerk, M., K. Wilson, and M. Pavao-Zuckerman. 2003. Conceptual models as tools for communication across disciplines. Conservation Ecology 7(3):8: http://www.consecol.org/vol7/iss3/art8/

The CEMs for species covered under the LCR MSCP are based on, and expand upon, methods developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The ERP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the National Marine Fisheries Service. The Bureau of Reclamation (Reclamation) participates in this program. (See attachment 1 for an introduction to the CEM process.)

Many of the LCR MSCP covered species are migratory. These models only address the species' life history as it relates to the lower Colorado River and specifically those areas that are potentially influenced by LCR MSCP land management. The models DO NOT take into account ecological factors that influence the species at their other migratory locations.

Finally, in determining the spatial extent of the literature used in these models, the goals and objectives of the LCR MSCP were taken into consideration. For species whose range is limited to the Southwest, the models are based on literature from throughout the species' range. In contrast, for those species whose breeding range is continental (e.g., yellow-billed cuckoo [*Coccyzus americanus occidentalis*]) or west-wide, the models primarily utilize studies from the Southwest.

How to Use the Models

There are three important elements to each CEM:

(1) The narrative description of the species' various life stages, critical biological activities and processes, and associated habitat elements.

(2) The figures that provide a visual snapshot of all the critical factors and causal links for a given life stage.

(3) The associated workbooks. Each CEM has a workbook that includes a worksheet for each life stage.

This narrative document is a basic guide, meant to summarize information on the species' most basic habitat needs, the figures are a graphic representation of how these needs are connected, and the accompanying workbook is a tool for land managers to see how on-the-ground changes might potentially change outcomes for the species in question. Reading, evaluating, and using these CEMs requires that the reader understand all three elements; no single element provides all the pertinent information in the model. While it seems convenient to simply read the narrative, we strongly recommend the reader have the figures and workbook open and refer to them while reviewing this document.

It is also tempting to see these products, once delivered, as "final." However, it is more accurate to view them as "living" documents, serving as the foundation for future work. Reclamation will update these products as new information is available, helping to inform land managers as they address the on-the-ground challenges inherent in natural resource management.

The knowledge gaps identified by these models are meant to serve only as an example of the work that could be done to further complete our understanding of the life history of the LCR MSCP covered species; however, this list can in no way be considered an exhaustive list of research needs. Additionally, while identifying knowledge gaps was an objective of this effort, evaluating the feasibility of addressing those gaps was not. Finally, while these models were developed for the LCR MSCP, the identified research needs and knowledge gaps reflect a current lack of understanding within the wider scientific community. As such, they may not reflect the current or future goals of the LCR MSCP. They are for the purpose of informing LCR MSCP decision making but are in no way meant as a call for Reclamation to undertake research to fill the identified knowledge gaps.

John Swett, Program Manager, LCR MSCP
Bureau of Reclamation
September 2015

Executive Summary

This document presents a conceptual ecological model (CEM) for the Townsend's big-eared bat (*Corynorhinus townsendii*), an evaluation species for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Bureau of Reclamation (Reclamation). The LCR MSCP planning area includes all of the Colorado River from Separation Canyon (lower Grand Canyon) to the U.S.-Mexico border and the adjacent floodplain, the full pool elevations of the three main reservoirs (Lakes Mead, Mohave, and Havasu) along the river, and the lower ends of the Virgin and Bill Williams Rivers inundated by these three main reservoirs (Reclamation 2004). The CEM methodology expands on that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read the attachment before continuing with this document.)

The CEM addresses the overall landscape used by Townsend's big-eared bats along the lower Colorado River (LCR) valley, not just the portions that lie within the LCR MSCP planning area. The CEM also captures the reality that the life cycle of Townsend's big-eared bats in the greater LCR ecosystem plays out in two distinct geographic zones: (1) the uplands where they find cold- and warm-season roosting sites and (2) the historic LCR floodplain and its immediate vicinity where they forage. LCR MSCP management responsibilities lie within its planning area, in cooperation with other Federal agencies, States, and Tribes. Management responsibilities for species conservation across the uplands surrounding the LCR MSCP planning area lie with these State, Tribes, and other Federal agencies.

The research questions and gaps in scientific knowledge identified through the modeling effort serve as examples of topics the larger scientific community could explore to improve the overall understanding of the ecology and conservation of Townsend's big-eared bats in the greater LCR ecosystem. These research questions and knowledge gaps may or may not be relevant to the goals of the LCR MSCP. As such, they are not to be considered guidance for Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

CONCEPTUAL ECOLOGICAL MODELS

CEMs integrate and organize existing knowledge concerning: (1) what is known about an ecological resource, with what certainty, and the sources of this information, (2) critical areas of uncertain or conflicting science that demand resolution to better guide management planning and action, (3) crucial

attributes to use while monitoring system conditions and predicting the effects of experiments, management actions, and other potential agents of change, and (4) how we expect the characteristics of the resource to change as a result of altering its shaping/controlling factors, including those resulting from management actions.

The CEM applied to PTBB expands on the methodology developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The model distinguishes the major life stages or events through which the individuals of a species must pass to complete a full life cycle. It then identifies the factors that shape the likelihood that individuals in each life stage will survive to the next stage in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

Specifically, the PTBB conceptual ecological model has five core components:

- **Life stages** – These consist of the major growth stages and critical events through which the individuals of a species must pass in order to complete a full life cycle.

- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals surviving to the next life stage (e.g., from juvenile to adult), and the number of offspring produced (fertility rate). The rates of the outcomes for an individual life stage depend on the rates of the critical biological activities and processes for that life stage.

- **Critical biological activities and processes** – These consist of the activities in which the species engages and the biological processes that take place during each life stage that significantly affect its life-stage outcomes rates. Examples of activities and processes for a bird species may include foraging, molt, nest site selection, and temperature regulation. Critical biological activities and processes typically are "rate" variables.

- **Habitat elements** – These consist of the specific habitat conditions, the quality, abundance, and spatial and temporal distributions of which significantly affect the rates of the critical biological activities and processes for each life stage. These effects on critical biological activities and processes may be either beneficial or detrimental. Taken together, the suite of natural habitat elements for a life stage is called the "habitat template" for that life stage. Defining the natural habitat template may involve estimating specific thresholds or ranges of suitable values for particular habitat elements, outside of which one or more critical biological activities or processes no longer fully support desired life-stage outcome rates—if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics—including human actions—that determine the quality, abundance, and spatial and temporal distributions of important habitat elements. Controlling factors are also called "drivers." There may be a hierarchy of such factors affecting the system at different scales of time and space (Burke et al. 2009). For example, the availability of suitable nest sites for a riparian nesting bird may depend on factors such as canopy closure, community type, humidity, and intermediate structure, which in turn may depend on factors such as the water storage-delivery system design and operation (dam design, reservoir morphology, and dam operations), which in turn is shaped by climate, land use, vegetation, water demand, and watershed geology.

This CEM identifies the causal relationships among these components for each life stage. A causal relationship exists when a change in one condition or property of a system results in a change in some other condition or property. A change in the first condition is said to cause a change in the second condition. The CEM method applied here assesses four variables for each causal relationship: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the certainty of a present scientific understanding of the effect. CEM diagrams and a linked spreadsheet tool document all information on the model components and their causal relationships. Software tools developed specifically for the LCR MSCP's conceptual ecological models allow users to query the CEM spreadsheet for each life stage and generate diagrams that selectively display query results concerning the CEM for each life stage.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

This CEM rests on the most recent species accounts by the LCR MSCP (2016) and NatureServe (2019) and comprehensive assessments by Gruver and Keinath (2006) and O'Shea et al. (2018). Additionally, it incorporates the findings of studies (Anderson et al. 2018; Elliott et al. 2017; Nelson and Gillan 2019; Smith 2018; Steel et al. 2018; Tobin and Chambers 2017; Weller et al. 2018) that these four reports do not address, including the findings of investigations in the Lower Colorado River Valley by and for the LCR MSCP over the past 10 years (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Brown 2010, 2013; Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Diamond 2012; Diamond et al. 2013; Hill 2018; LCR MSCP 2008, 2009; Maturango Museum and Brown-Berry Biological Consulting 2018; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2012, 2013; Brown, *in press*; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010). This

CEM also incorporates the expert knowledge of LCR MSCP biologists and information presented at annual Colorado River Terrestrial and Riparian meetings. Finally, Bunkley et al. (2015), Mikula (2015), Mikula et al. (2016), and Rodhouse et al. (2016) provide useful information on bat ecology in general; Faria et al. (2013), Kuzmin et al. (2012), and Stuchin et al. (2018) provide information on rabies transmission and effects in Townsend's big-eared bats. However, the purpose of this document is not to provide a literature review; rather, its purpose is to integrate current knowledge into a CEM for use in adaptive management.

The Townsend's big-eared bat CEM for the LCR identifies three life stages based on the aforementioned sources of information, and two or more life-stage outcomes for each life stage, as follows:

- Pups: pup growth, pup survival
- Juveniles: juvenile growth, juvenile survival
- Adults: adult growth, adult survival, adult fertility.

Chapter 2 defines and discusses these life stages and life-stage outcomes in detail.

The CEM identifies 14 critical biological activities and processes that affect 1 or more of these life-stage outcomes. Chapter 3 defines and discusses these critical biological activities and processes in detail. The 14 critical biological activities and processes are as follows, in alphabetical order: breeding, chemical stress, competition, disease, feeding, foraging, inter-site movement, maternal care, mechanical stress, predation, roosting: cold season, roosting: interim, roosting: warm season, and thermal stress. The reasoning for including these 14 critical biological activities and processes parallels the reasoning recently applied to CEMs for three other bat species in the Lower Colorado River Valley: western red bats (*Lasiurus blossevillii*), western yellow bats (*Lasiurus xanthinus*), and California leaf-nosed bats (*Macrotus californicus*) (Braun and Unnasch 2020a, 2020b, 2020c).

The CEM distinguishes 12 habitat elements that affect the rates, timing, magnitude, distribution, or other aspects of 1 or more critical biological activities or processes for 1 or more life stages. Chapter 4 defines and discusses these habitat elements in detail. The 12 habitat elements are as follows, in alphabetical order: anthropogenic disturbance; arthropod community; caves and cave analogs; chemical contaminants; fire regime; infectious agents; maternal care; monitoring, capture, handling; temperature; tree and shrub vegetation; vertebrate community; and water availability. The reasoning for including these 12 habitat elements again parallels the reasoning recently applied to CEMs for 3 other bat species in the Lower Colorado River Valley: western red bats, western yellow bats, and California leaf-nosed bats (Braun and Unnasch 2020a, 2020b, 2020c).

Finally, the CEM distinguishes eight controlling factors that affect the distribution, quality, composition, abundance, and other features of one or more of these habitat elements. Because the LCR ecosystem is highly regulated, the controlling factors almost exclusively concern human activities. Chapter 5 defines and discusses these controlling factors in detail. The eight controlling factors are as follows, in alphabetical order: conservation monitoring and research programs; fire management; habitat development and management; mining and mine management; nuisance species introduction and management; recreational use of caves and abandoned mines; surrounding land use; and water storage-delivery system design and operation. The reasoning for including these eight controlling factors again parallels the reasoning recently applied to CEMs for three other bat species in the Lower Colorado River Valley: western red bats, western yellow bats, and California leaf-nosed bats (Braun and Unnasch 2020a, 2020b, 2020c).

RESULTS

Nearly half (140 out of 308) of all proposed causal links in this CEM, across the three life stages combined, were rated as having unknown magnitude. This CEM proposes links with unknown magnitude based on basic principles of bat biology and expectations articulated in the literature, but for which no data or anecdotes are yet available for Townsend's big-eared bats or any similar or closely related species anywhere, let alone in the LCR ecosystem in particular. Further, causal links rated as having unknown magnitude comprise a much greater proportion of the links across the three life stages combined involving effects of life-stage outcomes (7 of 7) or critical biological activities or processes (59 of 89) compared to links involving effects of habitat elements (49 of 133) or controlling factors (25 of 79). This pattern reflects the lack of either anecdotes or formally collected evidence on many aspects of Townsend's big-eared bat biology and behavior that could help guide species or habitat management.

Similarly, nearly three quarters (224 of 308) of all proposed links in this CEM, across the three life stages combined, were rated as having low understanding; however, this ratio includes 140 links with a proposed rating of unknown for magnitude, which necessarily also received a rating of low for understanding. A more informative comparison of ratings for understanding focuses on links rated as having high, medium, or low magnitude. Fully half (84 of 168) of these latter links were rated as having low understanding as well. These results again reflect a lack of either anecdotes or formally collected evidence on many aspects of Townsend's big-eared bat ecology or biology or behavior that could help guide species or habitat management.

Nevertheless, an assessment of high-magnitude causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes, regardless of link understanding, highlights the following features of the CEM that may be useful for species or habitat management:

- The CEM proposes that seven controlling factors have direct, high-magnitude effects on one or more habitat elements. These are, in alphabetical order: conservation monitoring and research programs; fire management; mining and mine management; nuisance species introduction and management; recreational use of caves and abandoned mines; surrounding land use; and water storage-delivery system design and operation. Two of these factors—mining and mine management and recreational use of caves and abandoned mines—concern only the uplands where Townsend's big-eared bats in the greater LCR ecosystem seek warm- and cold-season roosts. One of the remaining factors, water storage-delivery system design and operation, concerns only the historic LCR floodplain within the LCR MSCP planning area. The CEM assigns a rating of high and medium understanding to most of these high-magnitude effects of controlling factors on habitat elements.

- The CEM proposes that seven habitat elements have direct, high-magnitude effects on one or more critical biological activities or processes in one or more life stages. These habitat elements are, in alphabetical order: anthropogenic disturbance; arthropod community; caves and cave analogs; maternal care (a habitat element for pups but a critical biological activity or process for adult females); temperature; tree and shrub vegetation; and vertebrate community. The CEM assigns a rating of high and medium understanding to most of these high-magnitude effects of habitat elements on critical biological activities and processes. Two of these seven—maternal care (a habitat element for pups but a critical biological activity or process for adult females) and temperature—are relevant to only to the uplands where Townsend's big-eared bats in the greater LCR ecosystem seek warm- and cold-season roosts. The other five are relevant both to these uplands and to the historic LCR floodplain and its immediate vicinity—the zone that encompasses the LCR MSCP planning area.

- The CEM proposes that six habitat elements have direct, high-magnitude effects on one or more other habitat elements, and thereby have (or additionally have) strong indirect effects on one or more critical biological activities or processes in one or more life stages. These six habitat elements are, in alphabetical order: anthropogenic disturbance; arthropod community; caves and cave analogs; monitoring, capture, handling; temperature; and water availability. Four habitat elements thus have high-magnitude *direct and indirect* effects on one or more critical biological activities or processes among the three life stages: anthropogenic

disturbance; arthropod community, caves and cave analogs, and temperature. The CEM assigns a rating of medium and low understanding to most of these high-magnitude effects of habitat elements on other habitat elements. The only two high-magnitude links between habitat elements with proposed ratings of high understanding are the links between air temperature and the fire regime, and between water availability and the tree and shrub vegetation, within the LCR planning area.

- The CEM proposes that six critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes among the three life stages. These six critical biological activities or processes are, in alphabetical order: breeding, with proposed high-magnitude effects on adult fertility; chemical stress, with proposed high-magnitude effects on adult growth and survival; feeding, with proposed high-magnitude effects on pup growth and survival; foraging, with proposed high-magnitude effects on both juvenile and adult growth and survival; maternal care, with proposed high-magnitude effects on adult fertility; and predation, with proposed high-magnitude effects on juvenile and adult survival. The CEM assigns a rating of low understanding to all these high-magnitude effects of critical biological activities or processes on life-stage outcomes. Three of these six—breeding, feeding, and maternal care—take place exclusively in the uplands where Townsend's big-eared bats in the greater LCR ecosystem seek warm- and cold-season roosts. Two of the other three—chemical stress and predation—are proposed to affect Townsend's big-eared bats in both the uplands and lowlands of the Lower Colorado River Valley. Only one of the six critical biological activities or processes with direct, high-magnitude effects on one or more life-stage outcomes, foraging, appears to take place in the historic LCR floodplain and its immediate vicinity.

- The CEM proposes that three critical biological activities or processes have direct, high-magnitude effects on one or more other critical biological activities or processes. These three thereby have (or additionally have) strong indirect effects on one or more life-stage outcomes across the three life stages. These three critical biological activities or processes are, in alphabetical order: foraging, with proposed high-magnitude effects on breeding and maternal care; and both cold- and warm-season roosting, with proposed high-magnitude effects on breeding. The CEM assigns a rating of low understanding to all these high-magnitude effects of critical biological activities or processes on other critical biological activities or processes.

The assessment of causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes also identifies numerous relationships with proposed intermediate (medium) and low magnitude. As knowledge about the species expands, the ratings of link magnitude for these proposed relationships, as well as for those currently assigned a high-magnitude rating, may change.

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for the Townsend's big-eared bat (*Corynorhinus townsendii*) (PTBB). The Townsend's big-eared bat is a covered, evaluation species for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Bureau of Reclamation (Reclamation). The LCR MSCP planning area includes all of the Colorado River from Separation Canyon (lower Grand Canyon) to the U.S.-Mexico border and the adjacent floodplain, the full pool elevations of the three main reservoirs (Lakes Mead, Mohave, and Havasu) along the river, and the lower ends of the Virgin and Bill Williams Rivers inundated by these three main reservoirs (Reclamation 2004).

The LCR MSCP acronym, PTBB, originally designated a subspecies, the Pale Townsend's big-eared bat (*C. t. pallescens*), in the LCR MSCP Habitat Conservation Plan (HCP) (Reclamation 2004). The HCP used such species acronyms to identify all of its formal conservation measures. The HCP focused on *C. t. pallescens* based on the contemporary understanding of bat systematics in the region (Arizona Game and Fish Department [AZGFD] 2003). However, genetic studies since completion of the HCP by Piaggio (Piaggio and Perkins 2005; Piaggio et al. 2009), Smith et al. (2008), and Anderson et al. (2018) have substantially altered the understanding of *Corynorhinus* systematics across North America. These genetic studies classify the members of this species in the lower Colorado River (LCR) valley as members of the widespread "Pacific" subspecies, *C. t. townsendii*, and identifies the *C. t. pallescens* subspecies as having a smaller, geographically more limited range that extends no further west than northeastern Arizona. Not all recent studies accept this reclassification: For example, the AZGFD (2019) continues to classify all observations in the Lower Colorado River Valley as *C. t. pallescens*, while Elliott et al. (2017), O'Shea et al. (2018), and NatureServe (2019) do not distinguish subspecies when discussing occurrences in southeastern California and western Arizona. Reports prepared by and for the LCR MSCP since 2009 (Berry et al. 2017; Broderick 2016; Brown 2010; Calvert 2016a, 2016b; Hill 2018; LCR MSCP 2016, 2017; Mixan and Diamond 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b) identify the species of concern in the Lower Colorado River Valley simply as *C. townsendii* without subspecies designation, but they retain the original acronym. This document simply identifies the species by its most common name, Townsend's big-eared bat. The literature reviewed for this CEM does not identify ecological differences among subspecies that could have implications for species or habitat management in the greater LCR ecosystem.

The purpose of this CEM is to help the LCR MSCP identify areas of scientific uncertainty concerning Townsend's big-eared bat ecology, the effects of specific stressors, the effects of management actions aimed at habitat restoration, and the methods used to measure Townsend's big-eared bat habitat and population

conditions. The CEM methodology follows that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012), with modifications. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read the attachment before continuing with this document.)

Townsend's big-eared bats historically roosted and currently roost within the greater Lower Colorado River Valley (Berry et al. 2017; Brown 2006, 2010, 2013; LCR MSCP 2016; Maturango Museum and Brown-Berry Biological Consulting 2018). As of 2017, the species is known to roost during the warm season on the west side of the valley only in the Gold Dollar Mine in the Riverside Mountains north of Blythe, California. A previous maternity colony location in the Mountaineer Mine, 4 kilometers (km) to the east in the same mountain range, was abandoned in August 2016 after being disturbed by a monitoring team (Maturango Museum and Brown-Berry Biological Consulting 2018). The disturbed bats moved to the Gold Dollar Mine. The species is also known to roost in two underground mines along the Planet Ranch reach of the Bill Williams River valley. One of these mines is a winter cold-air trap, resulting in its use by Townsend's big-eared bats as both a cold-season (hibernaculum) and a warm-season roosting site (Maturango Museum and Brown-Berry Biological Consulting 2018; Brown, *in press*).

All of these currently active roosting sites for Townsend's big-eared bats along the Lower Colorado River Valley lie in uplands outside the boundaries of the LCR MSCP planning area; however, the bats from these upland roosts forage mostly within and immediately around the historic LCR floodplain, where they also use interim roosting sites when night feeding. Their commuting routes and their zone of foraging and night roosting loosely encompasses the LCR MSCP planning area. The LCR MSCP therefore recognizes the Townsend's big-eared bats that use the planning area as an LCR population.

This CEM addresses the overall landscape used by the species along the Lower Colorado River Valley, not just the portions that lie within the LCR MSCP planning area. The CEM also captures the reality that the life cycle of Townsend's big-eared bats in the greater valley plays out in two distinct geographic zones: (1) the uplands where they find cold- and warm-season roosting sites and (2) the historic LCR floodplain and its immediate vicinity where they forage. LCR MSCP management responsibilities lie within its planning area, in cooperation with other Federal agencies, States, and Tribes. Management responsibilities for species conservation across the uplands surrounding the LCR MSCP planning area lie with these State, Tribes, and other Federal agencies.

This CEM rests on the most recent comprehensive species accounts (LCR MSCP 2016; NatureServe 2019) and conservation assessments (Gruver and Keinath 2006; O'Shea et al. 2018) for the species along with the findings of studies

(Anderson et al. 2018; Elliott et al. 2017; Nelson and Gillam 2019; Smith 2018; Steel et al. 2018; Tobin and Chambers 2017; Weller et al. 2018) that these four reports do not address, including the findings of investigations in the Lower Colorado River Valley by and for the LCR MSCP over the past 10 years (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Brown 2010, 2013; Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Diamond 2012; Diamond et al. 2013; Hill 2018; LCR MSCP 2008, 2009; Maturango Museum and Brown-Berry Biological Consulting 2018; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2012, 2013; Brown, *in press*; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010). This CEM also incorporates the expert knowledge of LCR MSCP biologists and information presented at the annual Colorado River Terrestrial and Riparian (CRTR) meetings in 2014–17[2] (Broderick 2014; Brown 2015; Calvert 2014, 2015, 2016c, 2017; Mixan and Diamond 2014b; Ronning 2017; Rubin et al. 2014; Mixan 2015, 2016, 2017). Finally, Bunkley et al. (2015), Mikula (2015), Mikula et al. (2016), and Rodhouse et al. (2016) provide useful information on bat ecology in general; and Faria et al. (2013), Kuzmin et al. (2012), and Stuchin et al. (2018) provide information on rabies transmission and effects in Townsend's big-eared bats. However, the purpose of this document is not to provide a literature review; rather, its purpose is to integrate current knowledge into a CEM so it can be used for adaptive management.

This document is organized as follows: The remainder of chapter 1 briefly summarizes the reproductive ecology of Townsend's big-eared bats, describes more fully the purpose of the CEM, and introduces the underlying concepts and structure of the CEM. Succeeding chapters present and explain the CEM for the species within the Lower Colorado River Valley and identify possible implications of this information for management, monitoring, and research needs.

TOWNSEND'S BIG-EARED BAT REPRODUCTIVE ECOLOGY

Townsend's big-eared bats are non-migratory, year-round residents of western North America, mostly (but not exclusively) west of the Rocky Mountains from southern British Columbia, Canada, southward to northern Sonora, Mexico. The range of the Pacific subspecies, *C. T. townsendii*, in the continental United States extends from the Pacific coast eastward to southern Montana, western South Dakota, western Colorado, and western New Mexico, at elevations

[2] No annual CRTR meetings took place in 2018 and 2019 due to temporary closures of the Federal Government.

from sea level to 2,400 meters (m) (7,900 feet) but mostly around approximately 900 m (3,000 feet) (AZGFD 2003). The pale subspecies (*C. t. pallescens*) currently is recognized only in western Colorado and northeastern Arizona eastward through south-central Wyoming to western Kansas, western Oklahoma, and northwestern Texas. A southern subspecies (*C. t. australis*) is recognized in the Western United States in western Texas, southern New Mexico, and in the interior of Mexico as far south as Oaxaca (O'Shea et al. 2018). As noted above, the population in the Lower Colorado River Valley is identified either by the trinomen, *C. t. townsendii*, or simply by the binomen, *C. townsendii* (LCR MSCP 2016), although the AZGFD (2019) continues to classify this population using the trinomen *C. t. pallescens*. The species is classified as imperiled (Conservation Rank S2) in California and Nevada and vulnerable (Rank S3) in Arizona (NatureServe 2019).

The Townsend's big-eared bat fits the characterization by Mikula et al. (2016) that, "In general, bats are K-strategists with long life spans and small litter sizes (Kunz and Fenton 2003), and life-history traits directly related to effective avoidance of predation (Rydell et al. 1996; Speakman 1991a, 1995)" (also see Gruver and Keinath 2006). The four recent species accounts for Townsend's big-eared bats on which this CEM rests (Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; O'Shea et al. 2018) all cite the same older data, indicating a typical maximum lifespan of approximately 16 years in the wild, with an average lifespan and a possible generation time (average difference in age between parent and offspring) of approximately 5 years.

The literature (see reviews by Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; O'Shea et al. 2018) consistently reports a birth rate of only a single offspring per year among reproductive females; however, the annual proportion of females that reproduce can vary. O'Shea et al. (2018) note that estimates of this proportion are "… likely biased high by captures at maternity colonies." The authors cite records of 91 percent to 99 percent of the females being reproductive among individuals captured in maternity colonies, and 1 record of 9 (64 percent) reproductive individuals among 14 females captured over water outside their maternity colony. Investigators have not yet identified the factors that affect the annual rate of male or female reproductive activity among Townsend's big-eared bat populations (see chapter 2, "Adults" and chapter 3, "Breeding").

The publications and data reviewed by the four recent species accounts do not include data on embryo mortality but do provide estimates of post-natal, pre-weaning survival rates of 95 to 96 percent, juvenile survival rates of 38 to 54 percent, and adult annual survival rates of 70 to 80 percent (Gruver and Keinath 2006; O'Shea et al. 2018). Gruver and Keinath (2006) specifically note:

> *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.*

On the other hand, the estimates of survival rates among adults rest on recapture records for banded individuals returning to their natal maternity site. Such records represent the combined effects of both mortality and dispersal of individuals to other sites, not mortality alone (Anderson et al. 2018; Gruver and Keinath 2006; LCR MSCP 2016; O'Shea et al. 2018). Since some adult Townsend's big-eared bats—particularly males—do disperse to maternity sites other than their natal sites (Anderson et al. 2018), the adult survival figure of 70 to 80 percent must under-estimate actual adult survival.

Townsend's big-eared bats do not exhibit any obvious behaviors for avoiding predators either while roosting or in flight. For example, they do not vary their foraging behavior in any apparent response to variation in moonlight intensity, which would affect their visibility to sight predators (Gruver and Keinath 2006). On the other hand, their reported affinity for commuting to foraging areas and foraging along the edges of taller vegetation (see chapter 3, "Foraging" and chapter 4, "Tree and Shrub Vegetation") may help limit predation (see chapter 3, "Predation").

The inability of Townsend's big-eared bats to produce more than a single offspring per female per year necessarily limits the ability of local populations to recover from severe stress. Townsend's big-eared bats also appear to have relatively inflexible requirements for the caves or cave analogs (e.g., underground mines) in which they hibernate and, subsequently, birth and raise their offspring. Chapter 3 discusses these requirements. The species also appears to be highly sensitive to disturbances in the caves and underground mines it selects for hibernation and maternal care: Complete closures of caves and inactive underground mines (e.g., to prevent trespassing), scientific and recreational excursions into open caves and inactive underground mines, and reactivation of underground mines can all cause Townsend's big-eared bats to abandon a roosting site (Gruver and Keinath 2006; Maturango Museum and Brown-Berry Biological Consulting 2018; Brown, *in press*; Sherwin et al. 2000a).

Townsend's big-eared bats exhibit great flexibility in the types of vegetation communities in which they forage and the elevations at which they forage: They appear to be habitat generalists, foraging in the vegetation communities available within nighttime flying distance of a suitable roosting site (see chapter 3, "Foraging") rather than selecting caves and underground mines for their warm-season roosts based on the surrounding vegetation, with perhaps some affinity for

foraging in and immediately around the edges of shrub and tree vegetation with a mosaic of vertical and horizontal edges and gaps—canopy layers, canopy edges and gaps, and stand edges and gaps (Fellers and Pierson 2002; Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; Nelson and Gillam 2019; O'Shea et al. 2018). This kind of vegetation mosaic is more typical of mature woody shrub and tree vegetation, the loss of which poses another limitation on species distribution and survival. Townsend's big-eared bats are not known to forage in developed (i.e., urban, residential, commercial, or industrial) areas but have been observed foraging over pasture and rangeland, perhaps further indicating their flexibility (Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; Nelson and Gillam 2019; O'Shea et al. 2018; Rogers et al. 2006). Individuals in the Lower Colorado River Valley during foraging excursions have been tracked traveling across large expanses of irrigated farmland (Maturango Museum and Brown-Berry Biological Consulting 2018; Brown, *in press*); however, the published data from these tracking efforts are not sufficient (or have not yet been analyzed) to determine whether the tracked bats navigated around or across the open areas of individual fields, and/or whether the bats were foraging at those times or were only traveling to foraging areas or to night (feeding) roosts.

Townsend's big-eared bat males and females show strong but not exclusive fidelity to a limited number of bachelor and maternity roosting sites, respectively, in caves and mines within any given locality as (Sherwin et al. 2000a). Individuals may move between bachelor or maternity roosting sites during the warm season but limit these movements to a small group of sites. Such inter-site movement of individual bats is greater among mines than among caves for both bachelor and maternity colonies; greater among smaller mines than among larger mines or among caves in general; and less among maternity colonies than among bachelor colonies, with some females remaining in the same maternity roosting site throughout the warm season.

Townsend's big-eared bat females also show strong but not exclusive fidelity specifically to their natal maternity colony (philopatry). Anderson et al. (2018) use genetic data, including mitochondrial deoxyribonucleic acid (DNA) data, to document mostly male, but also some female, dispersal and gene flow between maternity colonies over distances up to 136 km across the Inyo-White Mountains in west-central California. They note that their results are consistent with findings of previous studies of wide-ranging (100–150 km) dispersal among populations and subspecies of *C. townsendii*, while also showing a step-wise reduction in gene flow with distance. The ability to disperse and exchange genes widely presumably maintains genetic diversity across populations, and helps the species recolonize areas abandoned due to previous episodes of local stress, once local conditions recover.

The Townsend's big-eared bat adaptation therefore combines a low birth rate per adult female with a 60- to 99-percent annual rate of reproduction among adult

females, limited or no obvious behaviors for predator avoidance, low mortality among pups and adults with moderate mortality among juveniles, and strong philopatry combined with at least some regular dispersal of adult males and occasional females over distances up to 100 to 150 km. At the same time, the species appears to be highly sensitive to disturbances affecting the roosting sites it needs for hibernation and maternity, and moderately sensitive to the extent and quality of foraging habitat available around its roosting sites, but with flexibility in the types of natural vegetation around which it will forage.

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

Adaptive management of natural resources requires a framework to help managers understand the state of knowledge about how a resource "works," what elements of the resource they can affect through management, and how the resource will likely respond to management actions. The "resource" may be a population, species, habitat, or ecological complex. The best such frameworks incorporate the combined knowledge of many professionals accumulated over years of investigations and management actions. CEMs capture and synthesize this knowledge (Fischenich 2008; DiGennaro et al. 2012). The CEM methodology followed here is a crucial foundation for carrying out effects analyses, as described by Murphy and Weiland (2011, 2014) and illustrated by Jacobson et al. (2016).

CEMs explicitly identify: (1) the variables or attributes that best characterize resource conditions, (2) the factors that most strongly shape or control these variables under both natural and altered (including managed) conditions, (3) the character, strength, and predictability of the ways in which these factors do this shaping/controlling, and (4) how the characteristics of the resource vary as a result of the interplay of its shaping/controlling factors.

By integrating and explicitly organizing existing knowledge in this way, a CEM summarizes and documents: (1) what is known, with what certainty, and the sources of this information, (2) critical areas of uncertain or conflicting science that demand resolution to better guide management planning and action, (3) crucial attributes to use while monitoring system conditions and predicting the effects of experiments, management actions, and other potential agents of change, and (4) how the characteristics of the resource would likely change as a result of altering its shaping/controlling factors, including those resulting from management actions.

A CEM thus translates existing knowledge into a set of explicit hypotheses. The scientific community may consider some of these hypotheses well tested, but others less so. Through the model, scientists and managers can identify which hypotheses, and the assumptions they express, most strongly influence management actions. The CEM thus helps guide management actions based on

the results of monitoring and experimentation. These results indicate whether expectations about the results of management actions—as clearly stated in the CEM—have been met or not. Both expected and unexpected results allow managers to update the model, improving certainty about some aspects of the model while requiring changes to other aspects, to guide the next cycle of management actions and research. The CEM, through its successive iterations, becomes the record of improving knowledge and the ability to manage the system.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The CEM methodology used here expands on that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The expansion incorporates recommendations of Burke et al. (2009), Kondolf et al. (2008), and Wildhaber et al. (2007, 2011) to provide greater detail on causal linkages and outcomes and explicit demographic notation in the characterization of life-stage outcomes (McDonald and Caswell 1993). Attachment 1 provides a detailed description of the methodology. The resulting model is a "life history" model, as is common for CEMs focused on individual species and their population dynamics (Wildhaber et al. 2007, 2011). That is, the CEM distinguishes the major life stages or events through which the individuals of a species must pass to complete a full life cycle, including reproducing, and the biologically crucial outcomes of each life stage. These biologically crucial outcomes minimally include the number of individuals recruited to the next life stage (e.g., juvenile to adult) or to the next age class within a single life stage, termed the recruitment rate, and the number of viable offspring produced, termed the fertility rate. The CEM then identifies the factors that shape the rates of these outcomes in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

The PTBB conceptual ecological model has five core components as explained further in attachment 1:

- **Life stages** – These consist of the major growth stages and critical events through which the individuals of a species must pass in order to complete a full life cycle.

- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals surviving to the next life stage (e.g., from juvenile to adult), and the number of offspring produced (fertility rate). The rates of the outcomes for an individual life stage depend on the rates of the critical biological activities and processes for that life stage.

- **Critical biological activities and processes** – These consist of the activities in which the species engages and the biological processes that take place during each life stage that significantly affect its life-stage outcomes rates. Examples of activities and processes for a bird species may include foraging, molt, nest site selection, and temperature regulation. Critical biological activities and processes typically are "rate" variables.

- **Habitat elements** – These consist of the specific habitat conditions, the quality, abundance, and spatial and temporal distributions of which significantly affect the rates of the critical biological activities and processes for each life stage. These effects on critical biological activities and processes may be either beneficial or detrimental. Taken together, the suite of natural habitat elements for a life stage is called the "habitat template" for that life stage. Defining the natural habitat template may involve estimating specific thresholds or ranges of suitable values for particular habitat elements, outside of which one or more critical biological activities or processes no longer fully support desired life-stage outcome rates—if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics—including human actions—that determine the quality, abundance, and spatial and temporal distributions of important habitat elements. Controlling factors are also called "drivers." There may be a hierarchy of such factors affecting the system at different scales of time and space (Burke et al. 2009). For example, the availability of suitable nest sites for a riparian nesting bird may depend on factors such as canopy closure, community type, humidity, and intermediate structure, which in turn may depend on factors such as the water storage-delivery system design and operation (dam design, reservoir morphology, and dam operations), which in turn is shaped by climate, land use, vegetation, water demand, and watershed geology.

The process of identifying the life stages, life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors for a CEM begins with a review of the LCR MSCP and other major accounts for the species of interest, accounts for better known but closely related or ecologically similar species, and LCR MSCP management concerns as expressed in the LCR MSCP Habitat Conservation Plan (Reclamation 2004) and annual work plans (LCR MSCP 2018a). The process also follows conventions for life history CEMs focused on individual species and their population dynamics in the relevant branch of zoology for the species of interest. Further, the process is guided by an overarching need to ensure that the CEM helps the LCR MSCP identify areas of scientific uncertainty concerning the ecology and specific habitat requirements of the species it has been charged with conserving, the effects of specific stressors on these species, the effects of specific management actions aimed at habitat and species conservation, and the appropriate methods with which to monitor species

and habitat conditions. Each CEM is developed in consultation with experts in the LCR MSCP and submitted in draft form for review by the LCR MSCP in order to ensure that the CEM meets management needs. Terminology for life stages, life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors is standardized across CEMs where feasible and appropriate.

The process of identifying the life stages for a CEM recognizes that the life cycle of any species can be divided into multiple life stages. There is no rule for how many life stages a CEM must include, and different scientists may lump together or divide up the life cycle into a different set of life stages. The process of identifying the life stages for the LCR MSCP conceptual ecological models takes into account the following two criteria for lumping versus splitting life stages. First, knowledge of the species in the Lower Colorado River Valley prior to river regulation and the general ecological literature for similar species indicates that there could be differences in habitat requirements, threats, behaviors, or management requirements for individuals in different portions of the life cycle. Second, a single life stage may encompass several age classes; however, unless there are strong ecological reasons to distinguish individual age classes or groups of age classes as separate life stages, the LCR MSCP conceptual ecological models combine different age classes into the fewest life stages that make good ecological sense.

As noted above, the process of identifying the life-stage outcomes for a CEM follows the conventions for life history CEMs focused on individual species and their population dynamics in the relevant branch of zoology for the species of interest. These conventions recognize three possibilities: (1) The outcomes for an individual life stage may consist exclusively of survival. For example, the outcome of a juvenile life stage may consist only of survival to become an adult. (2) The outcomes for an individual life stage may consist of both survival and participation in reproduction, when participation in reproduction constitutes a distinct life stage for the species. (3) Alternatively, the outcomes for an individual life stage may consist of both survival and fertility, the latter of which concerns the production of viable fertilized eggs in the absence of parental care or the production of viable newborn in the presence of parental care. This third possibility pertains either to a life stage in which all individuals participate in reproduction, or to a life stage that focuses only on some subset of adults that engages in reproduction in a single year, such as breeding adult. Several of the species of concern to the LCR MSCP are subject to management goals concerning their genetic integrity; however, the CEM methodology focuses only on demographic outcomes unless the LCR MSCP Adaptive Management Program specifically requests that the CEM also include outcomes related to genetic integrity.

The process of identifying the critical biological activities and processes for a CEM focuses on identifying three possibilities in the literature: (1) activities

necessary to achieve one or more life-stage outcomes, such as feeding, mating, migrating, avoiding or escaping hazards, or resting in (relatively) safe settings, (2) biological processes that individuals must undergo to achieve one or more life-stage outcomes, such as maturing sexually, developing adult morphology and strength, or mating, and (3) biological processes that individuals will experience during the life stage that affect their fitness or survival, such as encounters with predators and/or competitors or experiences with physical or physiological stress that reduces fitness. Critical biological activities and processes thus may be either beneficial or detrimental to fitness, survival, or reproduction. Critical biological activities and processes may affect life-stage outcomes directly or may affect them only indirectly through their effects on other critical biological activities or processes. For example, disease may not always result in death (i.e., may not always directly affect survivorship), but it may make an individual weaker or disoriented and, therefore, less able to forage or be more vulnerable to depredation.

Ordinarily, only the life-stage outcomes of an individual life stage—survival and fertility—affect demographic dynamics in the next life stage; however, in some circumstances, critical biological activities or processes for one life stage also may affect dynamics in the next life stage. Most commonly, such trans-generational dynamics involve patterns of parental investment in raising offspring. For example, preparing a nest for eggs, protecting the eggs during incubation, and caring for the nestlings after the eggs hatch are all critical biological activities for breeding adult birds that have energetic and other costs for these adults. At the same time, these activities constitute crucial features of the environment—i.e., habitat elements—for the eggs and nestlings that affect their access to food and vulnerability to predators.

The process of identifying the critical biological activities and processes for a CEM recognizes that the critical biological activities and processes for any species can be combined or split into different categories in different ways. A single critical biological activity or process may encompass several more specific variables, behaviors, or changes. There is no rule for how many critical biological activities and processes a CEM must include or for determining which specific variables, behaviors, or changes to lump together under the heading of a single critical biological activity or process and which to split under separate headings. As with the process of identifying the life stages for the LCR MSCP conceptual ecological models, the process of identifying the critical biological activities and processes for a CEM looks for information on the species within its historic range and information in the general ecological literature for similar species indicating that there could be differences in habitat requirements, threats, or management requirements for different possible critical biological activities or processes.

The process of identifying the habitat elements for each life stage in a CEM focuses on identifying physical or biological environmental conditions that: (1) are necessary or beneficial for the successful participation of individuals of a

life stage in particular beneficial critical biological activities or processes, (2) may limit or prevent the successful participation of individuals of a life stage in particular beneficial critical biological activities or processes, or (3) may result in the participation of individuals of a life stage in particular detrimental critical biological activities or processes. Habitat elements thus shape the rates of beneficial or detrimental critical biological activities or processes. Further, habitat elements may affect critical biological activities or processes directly, indirectly through their effects on other habitat elements, or both. For example, the herbaceous vegetation in a marsh may benefit an aquatic species directly by providing protective cover and plant litter on which the aquatic species may feed; or indirectly by helping maintain cooler water temperatures, stabilizing the marsh substrate, and providing habitat for insects on which the aquatic species also may feed; however, the same marsh vegetation may also provide habitat for invertebrate or vertebrate species that may prey on the aquatic species of interest.

The process of identifying the habitat elements for each life stage in a CEM also recognizes that the key physical or biological environmental conditions affecting the individuals of a life stage can be combined or split into different categories in different ways. A single habitat element may encompass several more specific variables or properties of the physical or biological environment. There is no rule for how many habitat elements a CEM must include or for determining which specific properties of the physical or biological environment to lump together under the heading of a habitat element and which to split under separate headings. The process of identifying the habitat elements for each life stage in a CEM lumps together properties of the physical or biological environment that closely covary with each other over space and time along the LCR, because these properties are shaped by the same controlling factors and laws of physics or chemistry, and/or because these properties strongly interact with each other and, therefore, are not independent. A CEM also may lump together properties of the physical or biological environment when there is not sufficient knowledge to split these properties into separate habitat elements in ways that would help the LCR MSCP manage the species of concern. Finally, the CEMs lump together properties of the physical or biological environment that have similar effects or management implications across multiple life stages even if these effects or implications differ in their details between life stages. Lumping together such closely related properties under the heading for a single habitat element across all life stages makes comparison and integration of the CEMs for the individual life stages across the entire life cycle less difficult. On the other hand, a CEM may split properties of the physical or biological environment into separate habitat elements if they do not meet any of these criteria.

Finally, the process of identifying the controlling factors for each life stage in a CEM focuses on environmental conditions and dynamics—including human actions—that (1) determine the quality, abundance, and spatial and temporal distributions of important habitat elements and (2) are within the scope of potential human manipulation, most particularly manipulation by the LCR MSCP

and its conservation partners along the Lower Colorado River Valley. The specific or "immediate" controlling factors identified in a CEM necessarily exist and vary in a larger context of human institutions and policies and both short- and long-term dynamics of climate and geology; however, the CEM does not address this larger context. The process of identifying the controlling factors for each life stage in a CEM also recognizes that a controlling factor may affect a habitat element directly, or may do so indirectly, through its effects on either another controlling factor or another habitat element.

The process of identifying the controlling factors for each life stage in a CEM also recognizes that the key drivers affecting the habitat elements for that life stage can be combined or split into different categories in different ways. A single controlling factor may encompass several more specific variables or human activities. There is no rule for how many controlling factors a CEM must include. The process of identifying the controlling factors for each life stage in a CEM lumps together types of human activities in particular that closely covary with each other over space and time along the LCR because of the institutions and policies driving them and/or because these activities strongly interact with each other and, therefore, are not independent. A CEM also may lump together human activities when there is not sufficient knowledge to split these into separate categories in ways that would help the LCR MSCP manage the species of concern. Finally, the CEMs lump together human activities as controlling factors when these activities have similar effects or management implications across multiple life stages and across multiple species of concern to the LCR MSCP, even if these effects or implications differ in their details between life stages and species. Lumping together such closely related activities under the heading for a single controlling factor across multiple species and multiple life stages of these species makes comparison and integration of the CEMs across the LCR MSCP less difficult.

Each CEM not only identifies these five components for each species, but it also identifies the causal relationships among them that affect life-stage outcome rates. Further, the CEM assesses each causal linkage based on four variables to the extent possible with the available information: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the status (certainty) of a present scientific understanding of the effect. Attachment 1 provides detailed definitions and criteria for assessing these four variables for each causal link. Each CEM attempts to include all possible "significant" causal linkages among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes for each life stage. "Significant" here means that, based on the available literature and knowledge of experts in the LCR MSCP, the linkage has been proposed to exist or appears reasonably likely to exist and to have the potential to affect management of the species.

The CEM for each life stage thus identifies the causal relationships that most strongly support or limit the rates of its life-stage outcomes, support or limit the rate of each critical biological activity or process, and support or limit the quality, abundance, and distribution of each habitat element (as these affect other habitat elements or affect critical biological activities or processes). In addition, the model for each life stage highlights areas of scientific uncertainty concerning these causal relationships, the effects of specific management actions aimed at these relationships, and the suitability of the methods used to measure habitat and population conditions. Attachment 1 provides further details on the assessment of causal relationships, including the use of diagrams and a spreadsheet tool to record the details of the CEM and summarize the findings. Software tools developed in association with these CEMs allow users to query the CEM spreadsheet for each life stage and generate diagrams that selectively display query results concerning the CEM for each life stage. For example, a query may selectively identify all links with proposed high magnitude but low understanding or identify the critical biological activities or processes for a life stage with the greatest number of poorly understood drivers or effects.

Chapter 2 – Townsend's Big-eared Bat Life-Stage Model

A life stage consists of a biologically distinct portion of the life history of a species during which individuals undergo distinct developments in body form and function, engage in distinct behaviors, use distinct sets of habitats, and/or interact with their larger ecosystems in ways that differ from those associated with other life stages. This chapter proposes a life-stage model for Townsend's big-eared bats in the Lower Colorado River Valley on which to build the CEM. Except where noted, the information in this chapter is from the recent comprehensive species accounts by the LCR MSCP (2016) and NatureServe (2019) and conservation assessments by Gruver and Keinath (2006) and O'Shea et al. (2018). Table 1 and figure 1 summarize the proposed life-stage model for Townsend's big-eared bats in the valley.

Table 1.—Proposed life stages and life-stage outcomes for Townsend's big-eared bats in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Pups	• Pup growth • Pup survival
2. Juveniles	• Juvenile growth • Juvenile survival
3. Adults	• Adult growth • Adult survival • Adult fertility

INTRODUCTION TO THE TOWNSEND'S BIG-EARED BAT LIFE CYCLE

The life cycle of the Townsend's big-eared bats is similar to that of other cave-dwelling bats in North America, with pup, juvenile, and adult life stages. Female and male Townsend's big-eared bats have slightly different life histories, as described later in this chapter and in chapter 3; however, it does not appear useful to track adult female and male life stages separately for the purposes of this CEM.

The Townsend's big-eared bat CEM recognizes a minimum of two life-stage outcomes for each of the three life stages—growth and survival. The CEM applies the term, growth, to both (a) morphological and physiological development and (b) the maintenance of body mass and condition (health) in the face of the stresses of daily life, fluctuations in food intake, and hibernation.

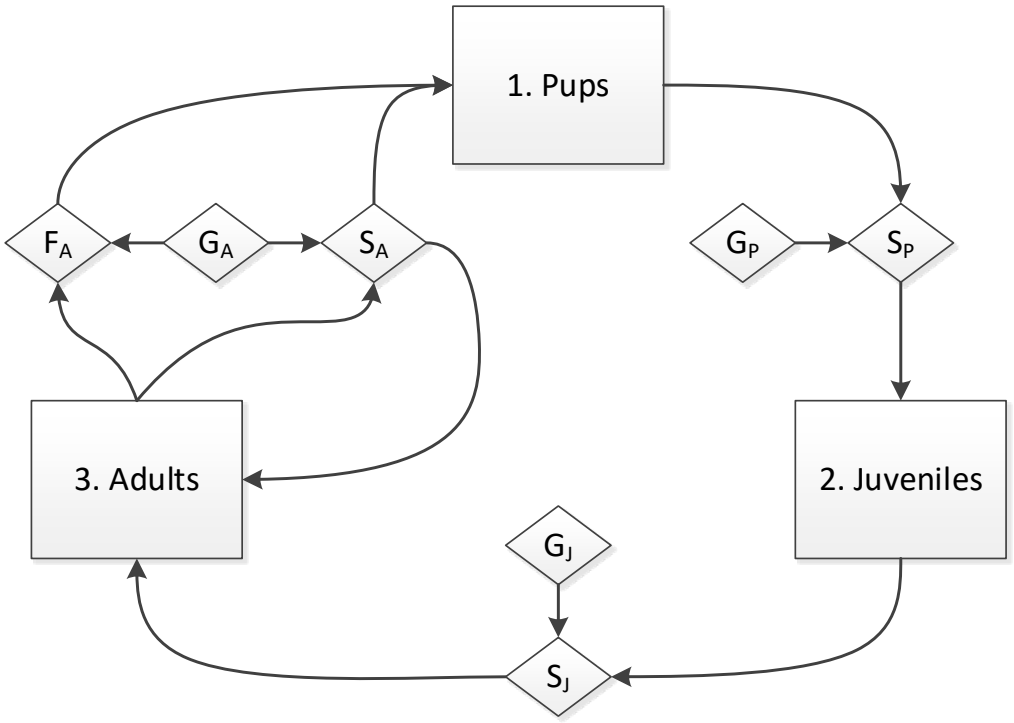

Figure 1.—Proposed life history model for the Townsend's big-eared bat.
Explanation of figure 1: Squares indicate life stages, diamonds indicate life-stage outcomes, and arrows indicate life-stage transitions. In the diamonds, S = survival, G = growth, and F = fertility; subscripts indicate the life stages involved in each transition.

Pup growth includes morphological and physiological maintenance and development from birth to weaning; juvenile growth includes morphological and physiological maintenance and development from weaning to sexual maturity, including building fat stores to carry the individual through hibernation; and adult growth includes the continued development and/or maintenance of body mass, building fat stores to carry the individual through hibernation, and support of mating as well as subsequent gestation and lactation in females. Growth may be positive or negative and may occur at different rates in females versus males. Survival for pups and juveniles is the rate at which members of a local population survive through their entire life stage to enter—recruit to—the next life stage. Survival for adults is the rate at which individuals in a local population survive from year to year. The CEM recognizes fertility—the rate of birthing of viable pups per adult female—as an additional life-stage outcome for the adult stage. Figure 1 illustrates the interplay of growth, survival, and fertility through the Townsend's big-eared bat life history.

Pups

Reproductive female Townsend's big-eared bats in the Western United States gather in maternity colonies of 12 to 200 individuals beginning in March through April or later. Each successful pregnancy produces a single pup (see below, this chapter, "Adults") between May and July after a gestation period of 56 to 100 days. Pups at birth weigh approximately 25 percent of the mother's weight. The clusters of individuals in the maternity colonies provide collective thermal protection for the pups. Pups are volant after 2.5 to 3 weeks but remain with their mothers and may continue nursing up to 6 weeks of age. Schmidly and Bradley (2016) state (but cite no primary data) that pups reach nearly their full adult size by the time they are volant, suggesting a roughly fourfold increase in body mass during this life stage. Post-natal, pre-weaning mortality is estimated to be 4 to 5 percent.

Juveniles

Townsend big-eared bat young are considered juveniles (*aka* yearlings) after weaning. They appear to remain in their natal colonies until the adults leave to begin moving to their winter roosting sites (hibernacula; see below, this chapter, "Adults"). Females may breed—and, therefore, transition to adulthood—as early as 4 months after birth, while all other females and all males become reproductively active only in their second year. Gruver and Keinath (2006) state that juvenile male Townsend big-eared bats produce sperm only "… in small numbers, which apparently do not migrate into the epididymides." As a result, juvenile male Townsend big-eared bats do not exhibit the enlarged accessory glands of mature males in spring and late summer, and are thus "… effectively sterile until their second year." Male Townsend big-eared bats are effectively adults after they complete their first year. The juvenile life stage (i.e., following weaning) thus may span as little as 3 months or as many as 11 months, ending with their first season of reproductive activity or the end of their first year of life, whichever comes first. After their first winter, yearling males and non-reproductive females join so-called bachelor colonies, while reproductive females join maternity colonies (see below, this chapter, "Adults"). These colonies may be located in different parts of the same caves.

The literature reviewed for this CEM does not indicate when juveniles achieve full adult body weight and dimensions; however, if pups reach nearly their full adult size by the time they are volant, and may continue nursing even after becoming volant, it seems likely that juveniles are already nearly adult sized at the start of this life stage.

The literature reviewed for this CEM also does not identify any ways in which juvenile foraging or roosting behaviors or patterns of inter-site movement differ

from those of adults; however, the literature indicates that juveniles have not received much study as a separate life stage. Further, juveniles appear to experience higher rates of mortality than do adults, suggesting that they are subject to greater threats than are adults. Gruver and Keinath (2006) note:

> *The mortality rate of juvenile C. townsendii was estimated to be 38 to 54 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.*

These figures cited by Gruver and Keinath (2006) may over-estimate actual juvenile mortality (O'Shea et al. 2018) because they are derived from data on rates of return of banded juveniles to their natal sites. Some juveniles (particularly males) may not return to their natal warm-season sites, but instead disperse to others, as do some adults (Anderson et al. 2018), and the original mark-recapture studies may not have monitored all such sites. Nevertheless, the evidence indicates higher mortality among Townsend big-eared bat juveniles versus adults. The literature does identify factors that might explain this difference.

Adults

This CEM categorizes Townsend's big-eared bats as adults when they first become reproductively active or at the end of their first year of life, whichever comes first. Adults (and presumably juveniles as well; see above) follow a highly consistent pattern of seasonal activities and inter-site movements (see chapter 3, "Inter-Site Movement") as follows:

- Female and male adults gather together at hibernacula (*aka* winter or cold-season roosting sites) in caves and underground mines during the colder months (see chapter 3, "Roosting: Cold Season"). Arrivals begin in October, but some individuals do not arrive until January. Some individuals may rouse temporarily from hibernation and some of these may move to a different location within the same cave or underground mine, or to a different cave or underground mine, but then resume hibernation; however, Townsend's big-eared bats overall show high cold-season philopatry (site fidelity). Mate selection and mating take place either shortly before or after arrival at the hibernacula. Individual females may mate with multiple males, and individual males may mate with multiple females. The reproductive females then store the sperm to delay fertilization of their eggs until they ovulate in spring (see below, next

paragraph, and chapter 3, "Breeding"). Juvenile males do not participate in reproductive activities and some juvenile and adult females may also not participate (see chapter 3, "Breeding").

- The bats leave their hibernacula in February through March for two different types of destinations. Reproductive females head off to maternity colonies, while males and non-reproductive females head off to so-called bachelor colonies (see chapter 3, "Roosting: Warm Season"). (Adult males also occasionally occur in maternity colonies). Bachelor colonies may form in different parts of the same caves or underground mines that contain maternity colonies, or in different caves or underground mines altogether. Reproductive females ovulate upon joining their maternity colonies and release their stored sperm, resulting in the fertilization of a single egg (see chapter 3, "Breeding").

- The bats remain in maternity and bachelor colonies until September or later in autumn (when they head off to hibernacula). Females (before giving birth or after weaning) may move between maternity colonies, and males may move between bachelor colonies; however, such movements may be much more common for colonies in abandoned underground mines rather than in caves and mostly take place among a fixed, limited group of roosting sites in any given locality year after year (Sherwin et al. 2000a, 2000b). Overall, both female and male Townsend's big-eared bats show a strong tendency toward warm-season philopatry (site fidelity), including female fidelity specifically to their natal maternity site. The adults forage at night during this time (roughly March to September) (see chapter 3, "Foraging"). Lactating females return to their maternity colony to nurse the young several times through the night (see chapter 3, "Maternal Care"). Both males and females also may use special night roosts (*aka* feeding roosts) to consume larger prey close by to their foraging areas without returning all the way to their day roosts (i.e., maternity and bachelor colonies; see chapter 3, "Roosting: Interim").

- Adults (and presumably juveniles, too) may use so-called transient (*aka* intermediate or staging) sites as temporary daytime stopovers during their movements between their main cold- and warm-season homes (see chapter 3, "Roosting: Interim"). Adults, including newly reproductively mature females, may also stop at so-called swarming sites after leaving their maternity colonies, where they engage in mating displays, mate selection, and copulation before joining hibernacula (see chapter 3, "Breeding" and "Roosting: Interim"). Swarming sites may be located within the same caves that provide sites for hibernation, or they may be separate locations.

As noted above, Townsend's big-eared bats are strongly but not exclusively philopatric, particularly adult females with respect to their maternity colonies;

however, individuals from different natal sites clearly encounter each other at mating sites (swarming sites and hibernacula), resulting in widespread genetic mixing. Anderson et al. (2018) observed for the species in the Inyo-White Mountains, west-central California:

> *Mitochondrial data … all point to the ability of male and female bats to encounter and mate with individuals from different maternity colonies across the sampling region. How often and when gene flow is occurring is unknown, but it is important to point out that C. townsendii can live 16 years in the wild (Paradiso and Greenhall 1967) giving this species a generation time that could extend to multiple years such that potential gene flow opportunities need not happen frequently (i.e., every year).*

Anderson et al. (2018) examined both mitochondrial and nuclear genetic markers in their study in the Inyo-White Mountains. The nuclear markers show mixing dispersal over greater distances than do the mitochondrial markers, suggesting that adult male Townsend's big-eared bats may disperse geographically more widely or more often to mate than do adult females of the species (see chapter 3, "Breeding" and "Inter-Site Movement").

As noted earlier in this chapter, the literature reports annual adult survival rates of 70 to 80 percent (Gruver and Keinath 2006; O'Shea et al. 2018); however, as also noted above (this chapter), the estimates of survival rates among adults rest on recapture records for banded individuals returning to their natal maternity site. Such records represent the combined effects of both mortality and dispersal of individuals to other sites, not mortality alone. Since some adult Townsend's big-eared bats do disperse to new maternity sites from their natal sites (Anderson et al. 2018), the adult survival figure of 70 to 80 percent likely under-estimates actual adult survival.

Chapter 3 – Critical Biological Activities and Processes

Critical biological activities and processes consist of activities in which a species engages and biological processes that take place during each life stage that significantly shape the rate(s) of the outcome(s) for that life stage. Critical biological activities and processes are "rate" variables: The rate (intensity) of these activities and processes, taken together, determine the rate of recruitment of individuals from one life stage to the next.

This CEM identifies 14 critical biological activities and processes that affect 1 or more life stages. Some of these activities or processes differ in their details among life stages; however, grouping activities or processes across all life stages into broad types makes it easier to compare the individual life stages to each other across the entire life cycle. Table 2 lists the 14 critical biological activities and processes and their distribution across life stages.

Table 2.—Proposed critical biological activities and processes for Townsend's big-eared bats in the LCR ecosystem and their distribution among life stages
(Xs indicate the critical biological activities or processes that apply to each life stage.)

Life stage ➔ Critical biological activity or process 🡻	Pups	Juveniles	Adults
Breeding			X
Chemical stress	X	X	X
Competition	X	X	X
Disease	X	X	X
Feeding	X		
Foraging		X	X
Inter-site movement		X	X
Maternal care			X
Mechanical stress	X	X	X
Predation	X	X	X
Roosting: cold season		X	X
Roosting: interim		X	X
Roosting: warm season		X	X
Thermal stress	X	X	X

Except where noted, the information in this chapter is from the recent comprehensive species accounts by the LCR MSCP (2016) and NatureServe (2019) and conservation assessments by Gruver and Keinath (2006) and O'Shea et al. (2018). The following paragraphs discuss the 14 critical biological activities and processes in alphabetical order.

BREEDING

This critical biological activity or process consists of a suite of more specific biological activities and processes, including swarming and mate selection, mating (copulation), sperm storage, ovulation and fertilization, and gestation and birthing. It does not include maternal care, which this CEM addresses as a separate critical biological activity or process. Chapter 2 (see "Adults") summarizes the annual breeding cycle in the species. The rates of all steps in the breeding cycle may vary, and the factors shaping this variation are mostly not well understood.

O'Shea et al. (2018) note:

> *Not all female Townsend's big-eared bats breed in their first year of life, and young males probably do not mate at all during their first year (Pearson et al., 1952). Nine of 26 non-reproductive females in an intensive California study were yearlings, and nine of 34 (26 percent) of the known-age one-year-old females in that study were non-reproductive (Pearson et al., 1952). We are unaware of any other published literature with quantitative data concerning age at first reproduction or inter-birth intervals. Mating may occur in hibernation throughout the winter in multiple copulations, with subsequent sperm storage until ovulation and fertilization take place in spring (Pearson et al., 1952). Sex ratio at birth is 1:1 (Pearson et al., 1952).*

As also noted above (see chapter 1), not all adult females reproduce in any given year. O'Shea et al. (2018) cite records of 91 to 99 percent of the females being reproductive among individuals captured in maternity colonies, and 1 record of 9 (64 percent) reproductive individuals among 14 females captured over water outside their maternity colony. However, O'Shea et al. (2018) also note that such estimates are "… likely biased high by captures at maternity colonies." The literature reviewed for this CEM does not provide information on the factors that may affect whether a year-one female may be reproductive in her first year or whether an older female may be reproductive in a given year. Similarly, the literature underlying this CEM does not provide quantitative information on the proportion of males that are biologically able to mate in any given year.

Environmental perturbations may disrupt gestation and/or maternal care. Gruver and Keinath (2006) note:

> *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.*

Further, female Townsend's big-eared bats may quickly abandon a maternity site after anthropogenic disturbance, and "… mothers that abandon roosts may leave non-volant young behind. … Unless the young are fully weaned and volant, their chances of survival are low" (Gruver and Keinath 2006; Maturango Museum and Brown-Berry Biological Consulting 2018).

Adult male Townsend's big-eared bats seeking to copulate at a swarming site or hibernaculum "… perform a courtship ritual in which they emit twittering sounds while approaching a female and then rub the snout over the female's body" (LCR MSCP 2016). Such behavior suggests that the males are competing for mates. The storage of sperm for delayed fertilization in the species also may facilitate sperm competition (Orr and Zuk 2013).

CHEMICAL STRESS

Chemical stress consists of physiological and even anatomical disruptions to an organism as a result of exposure to chemical conditions outside some healthy range. Chemical stress may be acute or chronic; may directly result in mortality; may impair a range of bodily functions, making the affected individuals less fit and, therefore, vulnerable to mortality from other causes; or may impair reproduction. Organisms may be able to avoid or remove themselves from settings in which they sense chemically unsuitable conditions before those conditions cause impairment, but only if (a) the organism can detect these conditions and (b) the conditions are sufficiently localized to permit such avoidance or escape.

As with all bats, Townsend's big-eared bats in one or more life stages are vulnerable to chemical stress from several potential sources. The literature on Townsend's big-eared bats specifically mentions or proposes the following:

- Mortality or impaired health from exposure to soluble metals and mining industrial wastes due to roosting in abandoned underground mines, including drinking from contaminated waters within or associated with such underground mines (Gruver and Keinath 2006; O'Shea et al. 2018). Some metals may bioaccumulate in Townsend's big-eared bat body tissues (Gruver and Keinath 2006).

- Impaired health and reproduction from the ingestion of insects exposed to pesticides, including organochlorine compounds, and subsequent bioaccumulation of the pesticides and/or their breakdown products (Gruver and Keinath 2006). The risk arises because, although Townsend's big-eared bats may not forage substantially over agricultural areas where pesticides may be used to control insects (see below, this chapter, "Foraging"), they do forage around the edges of such areas, and insects from these areas may disperse into surrounding habitat. Further, aerial spraying of pesticides can result in contamination of adjacent, non-agricultural areas where Townsend's big-eared bats may forage. Townsend's big-eared bat pups appear to be particularly susceptible to the bioaccumulation of fat-soluble contaminants from their mothers' milk, and these body loads persist as the individuals mature, potentially resulting in reproductive impairment or failure (Gruver and Keinath 2006). As recently emphasized by the European Food Safety Authority (Hernández-Jerez et al. 2019), pesticide exposure poses a risk to all insectivorous bats worldwide.

- Townsend's big-eared bats may be susceptible to high rates of radon absorption when roosting in caves and abandoned uranium mines, "… but the health effects of such exposure remain unknown" (O'Shea et al. 2018).

Townsend's big-eared bats appear to obtain most or all of their water by drinking directly from surface water bodies. Gruver and Keinath (2006) note that "Bats drink by skimming the surface of calm water bodies, and they appear to avoid open water with too much clutter (i.e., vegetation)." As a result, bats require the presence (within a suitable travel distance) of surface water bodies large enough for skimming. This CEM recognizes hydration stress as a form of chemical stress (see chapter 4, "Water Availability").

COMPETITION

All species face competition from other species and other members of their own species for the resources they need to survive, grow, and reproduce, and they may face competition for mates as well. Competition with other species may constrain

survival and growth and the geographic distribution of a species. Competition among members of the same species results in natural selection on genetically based differences among individuals.

As noted above, this chapter (see "Breeding"), adult male Townsend's big-eared bats may compete to attract females for copulation. Further, the storage of sperm for delayed fertilization may facilitate sperm competition (Orr and Zuk 2013). Townsend's big-eared bat pups do not compete with each other for maternal care because the species only births a single pup per mother.

The evidence is ambiguous for whether the Townsend's big-eared bats compete with other bat species for food or roosting habitat. Insectivorous bats have evolved in close competition with each other for millions of years, resulting in extensive resource partitioning. Such partitioning includes targeting different types of prey, in different environmental settings, at different times of night (Gruver and Keinath 2006). Further, while Townsend's big-eared bats do not roost in the direct company of members of other bat species—i.e., Townsend's big-eared bat maternity, bachelor, and winter colonies do not contain members of other bat species—it is not uncommon for colonies of several bat species to occupy different locations within the same cave or abandoned underground mine. Gruver and Keinath (2006) list 17 species of bats known to occupy the same cave or abandoned underground mine sites with Townsend's big-eared bats (among all of its subspecies), including the "Mexican big-eared bat (*C. mexicanus*), big brown bat [*Eptesicus fuscus*], Allen's big-eared bat (*Idionycteris phyllotis*), California leaf-nosed bat (*Macrotus californicus*), southwestern myotis (*Myotis auriculus*), California myotis (*M. californicus*), western small-footed myotis (*M. ciliolabrum*), western long-eared myotis (*M. evotis*), little brown bat (*M. lucifugus*), Indiana bat (*M. sodalis*), fringed myotis (*M. thysanodes*), cave myotis (*M. velifer*), long-legged myotis (*M. volans*), Yuma myotis (*M. yumanensis*), western pipistrelle (*Pipistrellus hesperus*), eastern pipistrelle (*P. subflavus*), and Mexican free-tailed bat (*Tadarida brasiliensis*)."

DISEASE

Disease consists of physiological and even anatomical disruptions to an organism as a result of their exposure to one or more pathogens. Townsend's big-eared bats are susceptible to a range of pathogens, including parasites (see chapter 4, "Infectious Agents"). Non-lethal infections may make affected individuals vulnerable to mortality from other causes, and other sources of stress correspondingly may increase susceptibility to disease.

Townsend's big-eared bats can host the rabies virus (Stuchin et al. 2018). The literature reviewed for this CEM mostly does not document the incidence of

illness in Townsend's big-eared bats due to a rabies infection (Gruver and Keinath 2006); however, O'Shea et al. (2018) state and cite reports that Townsend's big-eared bats are subject to deaths from rabies.

Gruver and Keinath (2006) mention one study that found Townsend's big-eared bats hosting two species of fleas (*Nycteridopsylla vancouverensis* and *Myodopsylla palposa*) but with unknown effects. Further, "Lewis (1995) hypothesized that reduction of parasite loads should increase fitness and may partially explain roost-switching behavior" (Gruver and Keinath 2006). O'Shea et al. (2018) also state (with citations) that Townsend's big-eared bats have been found with infestations of a variety of ectoparasites and endoparasites, but without evidence of associated mortality. O'Shea et al. (2018) also note that, so far, the Townsend's big-eared bat has encountered the white-nose fungal syndrome across the entire range of its eastern subspecies and as far west as western Oklahoma and Texas without evidence of deleterious illness.

FEEDING

Townsend's big-eared bat pups obtain their food passively from their mothers, in contrast to juveniles and adults, which actively forage for their food. Feeding success for a pup depends on the foraging success and provisioning rate of its mother (see below, this chapter, "Maternal Care") and the health of the pup. As noted above, this chapter (see above, this chapter, "Competition"), Townsend's big-eared bat pups are born singly and do not need to compete for food with siblings in the same litter. As also noted above (see above, this chapter, "Breeding"), Townsend's big-eared bat mothers fleeing a maternity colony following anthropogenic disturbance may abandon their pups, and non-volant pups have no ability to feed themselves.

FORAGING

Foraging includes both the efforts taken to locate and capture prey and the efforts taken to commute between roosting and foraging sites. Townsend's big-eared bats forage almost exclusively on moths, focusing on small (6- to 12-millimeter [mm]) Noctuidae (e.g., owlet moths), Geometridae (geometer moths), Notodontidae (prominent moths), and Sphingidae (sphinx moths); however, they also may forage opportunistically on other, similarly sized prey items such as beetles (Coleoptera), flies (Diptera), true bugs, including cicadas (Hemiptera), wasps, bees, ants (Hymenoptera), and mayflies (Trichoptera). This CEM assumes that foraging among Townsend's big-eared bat juveniles closely resembles foraging among adults. Further, as summarized by LCR MSCP (2016):

> *Generally, Townsend big-eared bats take their prey in the air, although Howell (1920) notes evidence of foliage gleaning (Kunz and Martin 1982; Pierson et al. 1999). They are considered to be slow fliers and highly agile and maneuverable (Dalquest 1947; Hayward and Davis 1964; Findley et al. 1972). This species leaves their roosting sites to forage approximately 45 minutes after sunset (Clark et al. 1993). There have been two peaks of foraging activity observed one right after leaving the roost and a second that occurs close to sunrise the following morning (Cockrum and Cross 1964). Females in a maternity roost were recorded having three feeding periods throughout the night; they return to the roost after each feeding. As offspring matured, females decreased how often they returned to the roost; once the young mature, the females do not return until sunrise (Clark et al. 1993; Clark et al. 2002).*

Townsend's big-eared bats forage in locations up to 14 km from their daytime roosts, with adult females traveling greater distances to forage than do males. Data collected from radio tracking show that a pregnant *C. townsendii* can travel over 150 km in a night of foraging" (R. Sherwin, personal communication, in Piaggio et al. 2009). During their nocturnal foraging excursions, males, and females that are not caring for pups, typically fly in and out of so-called night or feeding roosts to consume prey items too large to be eaten in midflight. As discussed below (see this chapter, "Roosting: Interim"), these night roosts tend to be shallow features such as overhangs, which the bats use individually rather than in groups, and they tend to be located close to their foraging areas. O'Shea et al. (2018) cite one study in southeastern Idaho that found the bats using night roosts within 0.8 km of their foraging areas. On the other hand, the bats may not use separate night roosting sites if their day-roosting sites are located close enough to their foraging areas, although they may still consume their prey in different parts of the same cave or underground mine from where they roost during the day (López-González and Torres-Morales 2004).

Only eight Townsend's big-eared bats have been tracked while foraging along the Lower Colorado River Valley, all from Gold Dollar Mine in August 2016, after initial capture at Mountaineer Mine, 4 km to the east, resulting in very limited data on foraging distances or behaviors (Maturango Museum and Brown-Berry Biological Consulting 2018; Brown, *in press*). The survey in August 2016 was the first telemetry study of Townsend's big-eared bat foraging behavior and flight distance along the valley. The investigators found:

> *Townsend's big-eared bats captured at the Mountaineer Mine (bats quickly relocated to the Gold Dollar Mine) were tracked a maximum of 9.5 miles (15.2 km) from the roost with an MCP* [minimum convex polygon, the smallest area encompassing all tracked positions for all eight bats] *encompassing 38,355 ac (15,522 ha)…. The movement after roost emergence was directed to the northeast and east in a broader fan toward the LCR.*

Townsend's big-eared bats appear to select their foraging habitat based on what is available within a suitable distance of their daytime roosting sites (Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; Nelson and Gillam 2019; O'Shea et al. 2018; Rogers et al. 2006). This pattern presumably results from the spatially limited availability of suitable caves and cave analogs (cave-like structures such as underground mines; see chapter 4). However, given a range of options for vegetation types and conditions, Townsend's big-eared bats west of the Rocky Mountains show a greater affinity for certain vegetation conditions, as discussed in chapter 4 (see "Tree and Shrub Vegetation") (also see Fellers and Pierson 2002; Vizcarra 2011). Briefly, they show a greater affinity for foraging in and/or around patches of tree and shrub vegetation with (a) greater vertical structure (e.g., mosaics of canopy and understory of different heights (see "Acronyms and Abbreviations" at the beginning of this report) and (b) greater amounts of edge habitat, such as edges of canopy, edges of vegetation riparian woodlands, and interfaces of woodlands with shrublands. Riparian edges near surface water may offer especially abundant insect populations for foraging as a result of aquatic insect productivity (Blakey et al. 2017; Hagen and Sabo 2012, 2014; Rubin et al. 2014). In contrast, Nelson and Gillam (2019) found that Townsend's big-eared bats in North Dakota foraged more often at sites located farther from water and more often at sites with less canopy cover compared to sites used by other bats in their study area.

As noted in chapter 1, Townsend's big-eared bats are not known to forage in developed (i.e., urban, residential, commercial, or industrial) areas; however, they have been observed foraging over pasture and rangeland, consistent with their overall flexibility in foraging habitat (Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; Nelson and Gillam 2019; O'Shea et al. 2018; Rogers et al. 2006). On the other hand, it is not clear if they avoid croplands. The individual foraging bats tracked in the Lower Colorado River Valley in August 2016 also traveled across large expanses of irrigated crops (Maturango Museum and Brown-Berry Biological Consulting 2018; Brown, *in press*). Unfortunately, the published data from these tracking efforts in the valley are not sufficient (or have not yet been analyzed) to determine whether the tracked bats navigated around or across the open areas of individual fields and/or whether the bats were foraging at those times or were only traveling to foraging areas or to night (feeding) roosts. Fellers and Pierson (2002) demonstrate the level of spatial precision required and a suitable sampling design for obtaining data on such details of Townsend's big-eared bat foraging navigation. The literature does not indicate whether Townsend's big-eared bats may forage in or around orchards.

The apparent affinity of the species for foraging along habitat edges, at least west of the Rocky Mountains, including in the Lower Colorado River Valley, affects the likelihood of their capture in mist nets placed in edge versus more homogeneous vegetation settings (Calvert 2010a, 2010b, 2014, 2016a, 2016b; Hill 2018; LCR MSCP 2008). This affinity also may help limit predation (see chapter 3, "Predation"). Townsend's big-eared bat echolocation calls during

foraging are notoriously faint (Steel et al. 2018), resulting in their being called a whispering bat. This behavior also affects the likelihood of their detection during foraging: Their low-decibel calls can only be detected and accurately distinguished when they fly within a limited distance of an acoustic monitoring station.

INTER-SITE MOVEMENT

Townsend's big-eared bats do not migrate but nevertheless exhibit four kinds of inter-site movement, as summarized in chapter 2 (see "Adults") (Anderson et al. 2018; Gruver and Keinath 2006; LCR MSCP 2016; NatureServe 2019; O'Shea et al. 2018; Sherwin et al. 2000a, 2000b). This critical biological activity or process concerns movements between sites where the bats roost for one or more consecutive days, including maternity and bachelor sites and hibernacula, and does not concern movements between such sites and night feeding sites during foraging excursions (see above, this chapter, "Foraging").

The four kinds of inter-site movement among Townsend's big-eared bats are as follows:

1. From their hibernacula to warm-season roosting sites, either maternity sites for reproductive females or bachelor sites for males and non-reproductive females. The bats may stop at so-called staging or intermediate roosting sites en route. The reproductive females may return to their natal maternity sites, while the males and non-reproductive females may return to sites near their natal sites; however, some individuals may disperse to other localities, with males possibly dispersing across greater distances than do females. The term "dispersing" here denotes movement to a location different from the one to which the majority of an individual's closest biological kin typically travel.

2. From one warm-season roosting site to another, including but not always or even necessarily following some anthropogenic disturbance. Such movements are apparently more frequent among individuals roosting in underground mines compared to caves, more common among smaller mines than among larger ones, and more common among males than among females. Most such movements involve relocations to sites within the same cave or underground mine or to another nearby cave or underground mine, with each individual moving among the same, limited number of sites over the course of their life, although not necessarily in the identical rotation every year.

3. From their warm-season roosting sites to hibernacula. Again, the bats may stop at so-called staging or intermediate roosting sites en route, which in this case may also include so-called swarming sites separate from the

destination hibernacula. Both sexes may return to the same hibernacula they used in their first year of life; however, again, some individuals may disperse to other localities, with males possibly dispersing across greater distances than do females. Again, the term "dispersing" here denotes movement to a location different from the one to which the majority of an individual's closest biological kin typically travel.

4. From one cold-season roosting site to another, such as following some anthropogenic disturbance. Such movements again are apparently more frequent among individuals roosting in underground mines compared to caves. Again, most such movements involve relocations to sites within the same cave or underground mine or to another nearby cave or underground mine.

The distances typically traveled during each of these types of movement may be as small as a few meters, from one location to another within the same cave or underground mine (López-González and Torres-Morales 2004; Schmidly and Bradley 2016), up to approximately 30 km or even up to 100–150 km (Piaggio et al. 2009). As discussed above (see chapter 1, "Townsend's Big-eared Bat Reproductive Ecology" and chapter 2, "Adults"), nuclear and mitochondrial DNA data demonstrate mostly male, but also some female, dispersal between maternity colonies over distances up to 136 km across the Inyo-White Mountains in west-central California, with a step-wise reduction in gene flow with distance (Anderson et al. 2018). These findings are consistent with those of previous studies indicating wide-ranging (100–150 km) dispersal among Townsend's big-eared bats in the Western United States. However, Piaggio et al. (2009) also report, "…our data suggest gene flow between *C. t. pallescens* and *C. t. townsendii* roosts that are at least 310 km apart, which may indicate longer distance movements than previously identified."

Townsend's big-eared bats have specific affinities for subterranean habitat conditions at the locations where they establish their maternity and bachelor colonies and hibernacula (see below, this chapter, "Roosting: Cold Season" and "Roosting: Warm Season"; also see chapter 4, "Caves and Cave Analogs"). If a cave or underground mine provides suitable conditions for maternity and bachelor colonies and hibernacula, in different sections of the same cave or underground mine, at least some bats may use the site year round, merely changing their interior location with the season (López-González and Torres-Morales 2004).

The literature indicates a relatively solid understanding of the factors shaping the timing, frequency, and distances for only some types of inter-site movements:

- The major seasonal movements, from cold-season to warm-season roosts, and vice versa, appear to be nearly synchronous regardless of latitude, altitude, or ecological setting. This pattern suggests that photoperiod and/or relative (but not absolute) seasonal changes in ambient air temperature at least partially constrain the timings of these major

movements. The distances involved in these major seasonal movements, in turn, appear to depend on the availability of caves or underground mines with suitable conditions (see chapter 4, "Roosting: "Cold Season" and "Roosting: Warm Season").

- The literature mentions several type of events that have been observed or are suspected to trigger movements from one cold-season roosting site to another or from one warm-season roosting site to another. The most commonly mentioned triggering events are disturbances by people entering a roosting site (Brown 2006) (see chapter 4, "Anthropogenic Disturbance"), including entering for scientific investigations (see chapter 4, "Monitoring, Capture, Handling"). Fellers and Pierson (2002) specifically note that, because Townsend's big-eared bats form maternity colonies consisting of clusters on open surfaces, they are particularly susceptible to disturbance such as from recreational caving.

- Gruver and Keinath (2006) also note, "Lewis (1995) hypothesizes that reduction of parasite loads should increase fitness and may partially explain roost-switching behavior." Additionally, Gruver and Keinath (2006) propose that, during hibernation, the bats may "change position within a hibernaculum or move to a nearby roost, presumably to find temperatures that are more suitable."

The literature reviewed for this CEM otherwise does not provide any systematic or anecdotal assessment of the possible causes of Townsend's big-eared bat dispersal, either its occurrence or the distances involved. For example, Sherwin et al. (2000a) specifically note that the set of bachelor and maternity roosting sites among which Townsend's big-eared bat males and females may include only a small number of sites over a small area or a larger number of sites over a larger area. They further note that the reasons for this variability were not evident in their study data or the research conducted up to the time of their study.

MATERNAL CARE

Maternal care of pups in maternity colonies includes feeding (nursing), and eventually weaning the pups, and providing a safe thermal environment. Bats generally groom themselves, and presumably maternal care therefore also includes grooming of pups, but the literature reviewed for this CEM does not address this topic for Townsend's big-eared bats. Adult females provide maternal care for their single pups as a critical biological activity or process. In turn, pups experience maternal care as a habitat element (see chapter 4, "Maternal Care").

Townsend's big-eared bat maternity colonies consist of tight clusters of up to 100 adult females with their pups (Gruver and Keinath 2006). Schmidly and Bradley (2016) note that "The bats hibernate in tight clusters, which may help stabilize body temperature against external changes in temperature." Presumably, such clustering and the resulting stabilization of body temperatures in maternity colonies also provide a stable thermal environment for the pups; however, Townsend's big-eared bats in the Western United States may form even larger colonies (up to 1,000 individuals) during hibernation than during maternal care, and colony size presumably may affect the extent to which a colony can stabilize body temperatures within the colony.

Townsend's big-eared bat maternal care apparently has some limits. As noted above, this chapter (see "Breeding"), mothers may leave their non-volant pups behind when they abandon a maternity site after anthropogenic disturbance. As also noted above (see "Breeding"), environmental perturbations may disrupt maternal care by affecting the ability of the adult females to care for their pups. Gruver and Keinath (2006) note:

> *When spring and summer temperatures are low and precipitation is high, [*female bats in maternity colonies*] 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.*

MECHANICAL STRESS

Bats in every life stage may suffer stress, physical injury, and outright physical destruction due to mechanical impacts and abrasions. Mechanical stress that does not result in mortality may leave the affected individuals more vulnerable to infections and mortality from other causes.

Townsend's big-eared bat pups may be injured if they fall from their roost, experience an unsuccessful attack by a predator, or are disturbed or handled by people. Juveniles and adults may be injured when disturbed by recreational or scientific intrusions into a roosting site, when captured and handled during mist-net monitoring, when investigators take tissue samples or attach identification bands or radio transmitters to some captured individuals for subsequent tracking, and potentially also when they escape direct contact with predators. The protocols for bat monitoring in the Lower Colorado River Valley are designed to minimize mechanical stress during observing, capture, handling, collection of tissue samples, attachment of identification bands or radio tracking devices, and release (Brown 2006; Hill 2018) (see chapter 4, "Monitoring, Capture, Handling").

Gruver and Keinath (2006) also note:

> *... 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). ... 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.*

Similarly, Tuttle and Moreno (2005) note for cave-dwelling bats in general, "… something as simple as partial blockage of a cave entrance by trees or shrubs can intolerably increase the risk of bats being injured or caught by predators." However, the literature reviewed for this CEM provides no data on the success of current field protocols for reducing the incidence or severity of injury to captured individuals of any bat species.

PREDATION

Townsend's big-eared bats presumably experience injury and mortality due to predation during every life stage, as do all wild animals. Every animal species has evolved strategies that permit its persistence despite predation, including specific behaviors, body features, and/or reproductive strategies that allow it to avoid, escape, deter, or counterbalance losses from predation.

As noted in chapter 1, Townsend's big-eared bats do not exhibit any obvious behaviors specifically for avoiding predators, either while roosting or in flight. For example, they roost in typically highly visible clusters on open surfaces of roost sites. Gruver and Keinath (2006) note that "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." Further, they do not vary their foraging behavior in response to variation in moonlight intensity and associated variation in the activity of sight predators. They also have only one pup per litter. A local population therefore cannot recover quickly from the effects of intense predation.

On the other hand, Townsend's big-eared bats may live up to approximately 16 years in the wild, and females may reproduce in their first year. As suggested by Gruver and Keinath (2006), adult male and non-reproductive female Townsend's big-eared bats may select their bachelor colony sites in part to minimize the risk of exposure to predators:

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.

Gruver and Keinath (2006) also suggest that Townsend's big-eared bats further reduce their risk of exposure to predators by commuting to foraging areas along linear forest edges and foraging along such edges (see chapter 4, "Tree and Shrub Vegetation"). The use of such edge habitat may limit the directions from which at least flying predators may attack.

Predators may attack Townsend's big-eared bats in four settings: (1) in their seasonal and interim (transient) roosts within caves, underground mines, crevices, and overhangs, (2) as the bats exit and enter the openings of caves and underground mines, (3) from the air during foraging and inter-site movement, and (4) from the ground, when their foraging activities bring them close to the ground. Further, because Townsend's big-eared bats forage and travel only at night, their vulnerability to predation in the latter three settings occurs only at night. The following paragraphs summarize the kind of species that potentially could prey on Townsend's big-eared bats in each of the four settings. Chapter 4 ("Arthropod Community," and "Vertebrate Community") provides more information on the species that potentially could prey on Townsend's big-eared bats in these settings.

Townsend's big-eared bats locate their cold- and warm-season roosts far enough into the interiors of caves and underground mines to find stable temperatures and humidities (see below, this chapter, "Roosting: Cold Season" and "Roosting: Warm Season"; also see chapter 4, "Caves and Cave Analogs"). Only a limited range of carnivorous climbing mammals and climbing reptiles may forage in such environments. Studies elsewhere have noted that large spiders (Nyffeler and Knörnschild 2013) and large centipedes (Molinari et al. 2005) also may prey on roosting bats. While no spiders or centipedes in the region of the Lower Colorado River Valley are known to do so, the subject has not been investigated, and numerous carnivorous arthropods occur in the caves and abandoned underground mines of the region (Elliott et al. 2017).

The surface openings of caves and underground mines may be low, narrow, or partially obstructed by trees or shrubs, and bats may crowd the resulting limited space at these entrances, especially when exiting in large numbers after sunset. Carnivorous birds, mammals, and reptiles can take advantage of these confined settings to prey on Townsend's big-eared bats as they exit or enter. As noted above, Tuttle and Moreno (2005) specifically mention for cave-dwelling bats in

general that "… something as simple as partial blockage of a cave entrance by trees or shrubs can intolerably increase the risk of bats being injured or caught by predators."

Avian predators are the main threat to Townsend's big-eared bats from the air during foraging and inter-site movement (Mikula et al. 2016). In fact, the literature review by Mikula et al. (2016) found:

> *Attacks on bats by diurnal raptors were found to be distributed globally and were present in the majority of extant raptor lineages. Attacks on bats by other diurnal birds were also occasionally recorded. Furthermore, the majority of extant bat families featured as prey. These results strongly suggest that predation by birds may act as a major factor affecting the scarcity of daytime activity in bats and as a driver in the evolution of bat nocturnality.*

The literature also identifies a few mammals that could prey on foraging Townsend's big-eared bats at ground level (see chapter 4, "Vertebrate Community"). Additionally, fishes and amphibians potentially can prey on bats at ground level when they come down at night to drink (Mikula 2015).

ROOSTING: COLD SEASON, WARM SEASON, INTERIM

As discussed in chapters 1 and 2, Townsend's big-eared bats engage in several different types of roosting activity over the course of their annual cycle. For purposes of this CEM, these critical biological activities are grouped into three categories: cold-season, warm-season, and interim roosting. The CEM recognizes each category of roosting as a separate critical biological activity. The species exhibits distinctive habitat affinities for each of these three critical biological activities, discussed in chapter 4 (see "Anthropogenic Disturbance," "Caves and Cave Analogs," "Temperature," "Tree and Shrub Vegetation," and "Water Availability").

Roosting: Cold Season

Female and male adults roost together during the cold season in hibernacula of 10–1,000 individuals, although investigators have observed individuals hibernating alone. Males often arrive before females. Arrivals begin in October, but some individuals do not arrive until January, which is when the colonies reach their maximum size. Hibernating individuals are mostly inactive, relying on body fat for energy; however, some individuals may rouse temporarily from hibernation, and some of these may move to a different location within the same

cave or underground mine, or to a different cave or underground mine, but then resume hibernation. Mating may take place either shortly before or after arrival at the hibernacula.

Roosting: Warm Season

The bats leave their hibernacula in February through March, relocating to two different types of warm-season roosting sites. Reproductive females relocate to maternity colonies, while males and non-reproductive females relocate to so-called bachelor colonies; however, adult males are occasionally observed in maternity colonies as well. Bachelor colonies may form in different parts of the same caves or underground mines that contain maternity colonies or in different caves or underground mines altogether. The bats remain in their maternity and bachelor colonies until September or later in autumn, after which time they relocate to hibernacula.

Reproductive females cluster together in their maternity colonies, which may include 10–100 adults. The clustering presumably helps provide thermal stability for the pups. The lactating females leave their maternity colonies at night to forage but return to the colony to nurse the young several times through the night. Gruver and Keinath (2006) further observe (also see chapter 4, "Temperature"):

> *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 warmer than random structures (Pierson and Rainey 1998).*

Warm-season, bachelor colonies are typically much smaller than the nearby maternity colonies, typically consisting of only a few individual bats. Bachelor colonies therefore are more numerous. Gruver and Keinath (2006) note:

> *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.*

The members of bachelor colonies leave their roosts at night to forage; however, unlike the members of maternity colonies, they may not return to the colony until the end of the night.

Females may move between maternity colonies before giving birth or after weaning. Males also may move between bachelor colonies over the course of a

single season; however, such movements may be much more common for colonies in abandoned underground mines rather than in caves (Sherwin et al. 2000a, 2000b). Gruver and Keinath (2006) note:

> *… 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.*

Roosting: Interim

Townsend's big-eared bats may engage in up to three other different, additional types of roosting activity either during the warm season or while moving between cold- and warm-season roosting sites. For purposes of this CEM, following Gruver and Keinath (2006), these three other types of roosting activity are grouped together as "interim" roosting activities. The three types of interim roosting activity are as follows:

- During their foraging excursions over the course of the warm season, both males and females use special night roosts (*aka* feeding roosts) to consume prey items too large to be eaten in midflight. This behavior allows the bats to remain close to their foraging areas over the course of the entire night without returning to their day roosts (see above, this chapter, "Foraging"). They may remain in their night roosts long enough to finish their meal before returning to foraging, or longer: As noted above, this chapter (see "Foraging"), Townsend's big-eared bats exhibit two peaks of foraging activity over the course of each night, one directly after leaving the roost and a second close to the end of the night. This bimodal pattern suggests that at least males remain in their temporary night roosts for up to a few hours, during the pause between the two peaks in foraging activity. As also noted above, however, females with immature pups return to their roost after each feeding but, "… As offspring matured, females decreased how often they returned to the roost; once the young mature, the females do not return until sunrise (LCR MSCP 2016)."

- Both males and females may use so-called transient (*aka* intermediate or staging) sites as temporary daytime stopovers during their movements between their main cold- and warm-season roosting sites. Gruver and Keinath (2006) note that the bats show little fidelity to individual transient sites while moving between warm- and cold-season roosting sites and that the use of transient sites "… 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."

- Adults, including newly reproductively mature females, may also stop at so-called swarming sites after leaving their maternity colonies to engage in mating displays, mate selection, and copulation before joining hibernacula. Swarming sites may be located within the same caves or underground mines that provide sites for hibernation, or they may be separate locations. Ingersoll et al. (2010) observed that Townsend's big-eared bats at swarming sites "… are very active at night, rousing frequently several times a night to fly within and between roosts."

THERMAL STRESS

Exposure to air temperatures outside their ranges of tolerance presumably render Townsend's big-eared bats in every life stage vulnerable to reduced metabolic rates, reduced growth, impaired performance, disease, stress, and mortality, as is the case with all bats. All bats expend energy to regulate their body temperatures through their metabolism and through behaviors to locate themselves in thermally less stressful environments while flying and resting; however, the bioenergetic costs of maintaining their metabolism and engaging in thermally protective behaviors also may reduce the energy available for growth and reproduction of bats in all life stages (Barclay and Harder 2003).

The entire annual cycle of roosting activities in Townsend's big-eared bats is thought to be an adaptation to the thermal conditions they face both in the open and within the caves and underground mines they select for roosting (Gruver and Keinath 2006; O'Shea et al. 2018). Their clustering behaviors in both hibernacula and maternity colonies, and within-season movements between maternity sites, are also thought to be adaptations to reduce risks of thermal stress (see above, this chapter, "Roosting"). Jones et al. (2009) provide evidence of the effects of extreme cold and heat on various bat species. This evidence includes a massive die-off of bat pups in Australia in 2006 due to extreme cold and a massive die-off of over 3,500 individuals of a mixed-species colony in New South Wales in 2002 due to extreme heat.

Chapter 4 discusses the available evidence on thermal preferences and tolerances among Townsend's big-eared bats. The literature mostly does not document the effects of thermal stress per se but rather mostly documents activities and behaviors that appear to have evolved to reduce exposure to potentially thermally stressful conditions.

Chapter 4 – Habitat Elements

Habitat elements consist of specific conditions in the biotic or abiotic environment; the quality, abundance, spatial and temporal distributions; or other properties of which significantly affect the rates of critical biological activities and processes for one or more life stages.

This chapter identifies 12 habitat elements that may affect 1 or more critical biological activities or processes among the 3 Townsend's big-eared bat life stages. Table 3 lists the 12 habitat elements and the critical biological activities or processes that they may *directly* affect across all life stages. Habitat elements may also directly affect each other.

Table 3.—Proposed habitat elements for Townsend's big-eared bats in the LCR ecosystem and the critical biological activities and processes they may directly affect
(Xs indicate which habitat elements may affect each critical biological activity or process.)

Critical biological activity or process ➔ / Habitat element ⬇	Breeding	Chemical stress	Competition	Disease	Feeding	Foraging	Inter-site movement	Maternal care	Mechanical stress	Predation	Roosting: cold season	Roosting: warm season	Roosting: interim	Thermal stress
Anthropogenic disturbance	X				X	X		X	X		X	X	X	
Arthropod community						X				X		X		
Caves and cave analogs											X	X	X	
Chemical contaminants		X												
Fire regime														X
Infectious agents				X										
Maternal care					X					X		X		X
Monitoring, capture, handling									X					
Temperature											X	X		X
Tree and shrub vegetation						X	X			X	X	X		
Vertebrate community			X							X	X	X	X	
Water availability		X									X	X		

Some of the habitat elements in this CEM differ in their details among life stages. For example, different species may prey on different life stages of Townsend's big-eared bats; however, using the same labels for the same general kinds of habitat elements across all life stages makes it possible to compare the CEMs for individual life stages across the entire life cycle.

The reasoning for including the 12 habitat elements again parallels the reasoning recently applied to CEMs for 3 other bat species in the Lower Colorado River Valley: western red bats, western yellow bats, and California leaf-nosed bats (Braun and Unnasch 2020a, 2020b, 2020c). Except where noted, the information in this chapter is from the recent comprehensive species accounts by the LCR MSCP (2016) and NatureServe (2019) and conservation assessments by Gruver and Keinath (2006) and O'Shea et al. (2018). The following paragraphs discuss the 12 critical biological activities and processes in alphabetical order.

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a short name, typically of only one to three words; however, each short name in fact refers to a longer, full name. For example, "fire regime" is the short name for "The frequency, timing, spatial extent, and intensity of fire in and around existing or potential Townsend's big-eared bat roosting and foraging habitat." The following paragraphs provide both the short and full names for each habitat element and a detailed definition, addressing the elements in alphabetical order.

ANTHROPOGENIC DISTURBANCE

Full name: **Noise and other physical disturbances associated with human activity in and around existing or potential Townsend's big-eared bat roosting and foraging habitat**. This element refers to the existence and level of human disturbance of Townsend's big-eared bat roosting habitat, including noise, intrusions, and physical contact with the bats. The disturbance of roost sites, including their entryways and immediate surrounding spaces, may be a leading cause of species decline. As noted in chapter 3 (see "Inter-Site Movement" and "Maternal Care"), Townsend's big-eared bats may abandon cold- or warm-season roosting sites where they have experienced anthropogenic disturbance, including abandoning non-volant pups in the process. O'Shea et al. (2018) note that the kinds of caves favored by the species for maternity roosting—"complex sites with multiple openings and multiple internal levels with large internal dimensions"—also are the types of caves that particularly attract human exploration and, therefore, experience more frequent human disturbance. In contrast, Townsend's big-eared bats do not appear to avoid or abandon foraging areas where they may encounter disturbances at night, except as a secondary effect of their avoiding developed areas and other types of unwanted habitat. Nighttime noise from

infrastructure and human activities in developed areas may disrupt echolocation and, thereby, interfere with foraging among some bat species (Bunkley et a. 2015); the subject has not been investigated among Townsend's big-eared bats.

ARTHROPOD COMMUNITY

Full name: **The taxonomic composition, size range, spatial and temporal distributions, and abundance of the arthropod community in and around existing or potential Townsend's big-eared bat roosting and foraging habitat**. The arthropods of concern may include moths, beetles, flies, mayflies, true bugs, including cicadas, wasps, bees, and ants that Townsend's big-eared bats may consume, as well as other arthropods that may compete with or prey on Townsend's big-eared bats, or otherwise contribute to ecological dynamics in and around their foraging or roosting sites. For example, herbivorous arthropods in general may affect ecological—particularly vegetation—dynamics in and around foraging areas.

Chapter 3 (see "Foraging") discusses the range of arthropod species on which Townsend's big-eared bats may feed. The species and abundances of such arthropods available at night necessarily affect Townsend's big-eared bat juvenile and adult foraging success and nutrition. There is growing literature on the arthropod communities at and around potential bat foraging sites in the Lower Colorado River Valley (Anderson 2012; Andersen and Nelson 2013; Eckberg 2011, 2012; Nelson 2009; Nelson and Wydoski 2013; Nelson et al. 2015; Ohmart et al. 1988; Pratt and Wiesenborn 2009, 2011; Rubin et al. 2014; Trathnigg and Phillips 2015; Wiesenborn 2010, 2012, 2013, 2014a, 2014b; Wiesenborn et al. 2008). A full review of this literature is beyond the scope of this CEM; however, it should be noted (see chapter 3, "Foraging") that the edges of riparian vegetation near surface water may offer especially abundant insect populations for foraging as a result of aquatic insect productivity in these settings (Blakey et al. 2017; Hagen and Sabo 2012, 2014; Rubin et al. 2014).

Predatory arthropods such as mantises, spiders, and wasps that prey on other arthropods may compete with Townsend's big-eared bats for food resources. Further, such arthropods may prey on these shared food resources by preying on their eggs and larvae or when the adult prey are resting on the ground or in vegetation. However, as noted above, a review of the potentially relevant literature and data on the arthropod communities along the Lower Colorado River Valley is beyond the scope of this CEM.

As discussed in chapter 3 (see "Predation"), studies elsewhere have noted that large spiders (Nyffeler and Knörnschild 2013) and large centipedes (Molinari et al. 2005) also may prey on roosting bats. While no spiders or centipedes in the region of the Lower Colorado River Valley are known to do so, the subject has not been investigated, and numerous carnivorous arthropods occur in the caves and abandoned underground mines of the region (Elliott et al. 2017). This CEM recognizes the possibility of arthropod predation on Townsend's big-eared bats in their roosting sites based on general ecological concepts.

Arthropods, particularly insects, can significantly affect vegetation dynamics in all ecosystems, including riparian communities. The effects of the non-native northern tamarisk beetle (*Diorhabda carinulata*) on saltcedar (*Tamarix* spp.) along the Colorado River Valley provides a particularly clear example. Resource managers intentionally released the beetle in 2001 in the Upper Colorado River Basin as a biocontrol for the invasive saltcedar (Bean and Dudley 2018). The beetle has spread widely, including down the valley into the LCR ecosystem, where it currently occurs as far south as the Imperial National Wildlife Refuge as of January 2019 (RiversEdge West 2019). Repeated defoliation by the beetle usually causes the canopy to die back within 1 to 4 years and causes plant death within 2 years or more depending on the site (Bean and Dudley 2018). The literature reviewed for this update does not document effects of native arthropods on riparian vegetation along the Lower Colorado River Valley, and a review of such information is beyond the scope of this CEM.

CAVES AND CAVE ANALOGS

Full name: **The types, locations, sizes, and other characteristics of natural caves and cave analogs that Townsend's big-eared bats use or potentially could use as roosting habitat**. As discussed in chapter 3 (see "Roosting"), Townsend's big-eared bats use caves and cave analogs as cold-season hibernacula, warm-season maternal and bachelor roosting sites, and interim roosting sites such as for night (*aka* feeding) roosting, transient (*aka* staging) roosting during movements between cold- and warm-season roosting sites, and swarming.

Natural caves used by Townsend's big-eared bats may be underground cavities and passages in any kind of "cavity forming rock (e.g., limestone, sandstone, gypsum, or volcanic)" (Brown 2006) with openings to the ground surface large enough for bats to fly in and out. Cave analogs (*aka* cave-like structures or features) used by Townsend's big-eared bats include natural overhangs and shallow cavities (*aka* rock shelters) in cliffs and other bedrock surface outcrops; short mining prospects; hollows in large trees; the adits, airways, cavities, and passageways of inactive underground mines; cave-like cavities under bridges; and rooms, particularly attics, in unused buildings. As noted by Brown (2006), "From

the perspective of many bat species, old mines are cave habitat and are now sheltering many large colonies." Maturango Museum and Brown-Berry Biological Consulting (2018) (also see Brown, *in press*) tracked several foraging individuals to buildings on Colorado River Indian Tribes [CRIT] lands in the Lower Colorado River Valley in August 2016.

Townsend's big-eared bats prefer broad, open overhead surfaces in caves and cave analogs on which to hang while they roost. They do not roost in cracks or crevices. When roosting during the daytime (i.e., in hibernacula or in maternal and bachelor roosts), they generally occupy areas of caves and cave analogs with nearly total darkness. As noted in chapter 3 (see "Inter-Site Movement"), at least some Townsend's big-eared bats may use a single cave or cave analog year round, merely changing their interior location with the season, if the overall feature provides suitable conditions for maternity and bachelor colonies and hibernacula, perhaps in different sections of the larger cave or underground mine (López-González and Torres-Morales 2004).

Gruver and Keinath (2006) summarize Townsend's big-eared bat use of caves and cave analogs in general as follows:

> *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 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).*

TheLCR MSCP (2016) further notes:

> *Maternity sites in northern Utah were found to be more complex than bachelor roost sites, having larger entrances and more openings. Maternity roosts in caves were found to be larger and more spatially stable than those in mines, which was probably due to the fact that caves were an older, more dependable resource (Sherwin et al. 2000b)... Unlike maternity colonies, bachelor (and non-reproductive female) roosting sites usually contain 1 to several individuals, although 1 site in Kentucky had more than 1,000 bats together in a bachelor roost (Pierson and Rainey 1998; Pierson et al. 1999; Sherwin et al. 2000b; Lacki et al. 1994). Humphrey and Kunz (1976) found a maximum of 6 males in a roost together, with an average of 2 bats, in a total of 25 caves. Along the LCR, males may be territorial and roost alone unless the site is very large (P. Brown 2005, personal communication). Bachelor roost selection is not as complex as it is for maternity colonies (Humphrey and Kunz 1976; Lacki et al. 1994; Sherwin et al. 2000b). Similar to maternity sites, Sherwin et al. (2000a, 2000b) found bachelor sites more temporally stable in caves than in mines, with an 89 percent chance of finding a bat on a subsequent night in caves compared to only a 38 percent chance of finding a bat at a mine roost.*

Townsend's big-eared bat night (feeding) roosts consist of caves or cave analogs close to foraging areas, into and out of which the bats can easily fly, that provide a suitable overhead surface onto which the bats can land and hold while feeding. As a result, their characteristics vary widely. Caves and cave analogs used as transient roosting (staging) sites have similarly widely varying characteristics.

Townsend's big-eared bat swarming generally occurs in the same caves or cave analogs where they subsequently hibernate but in different locations within these larger features. Ingersoll et al. (2010) compared swarming versus hibernation sites in numerous underground mines in western Colorado and found (also see below, this chapter, "Temperature"):

> *Daytime activity is suppressed during both periods by daily torpor. Both hibernacula and swarming roosts have particular thermal requirements associated with energetic optimization. Swarming roosts tend to have a higher minimum temperature than hibernacula, facilitating efficient arousal from torpor. Both roost types have low maximum temperatures, facilitating conservation of stored body fat resources.*

Townsend's big-eared bats may hibernate in the same caves or cave analogs where they also roost in the warm season or in caves or cave analogs with similar overall characteristics (López-González and Torres-Morales 2004). However, as noted below, this chapter (see "Temperature"), they hibernate in areas with different characteristics of temperature and humidity than the areas they prefer for maternal and bachelor roosting.

All roosting sites used by Townsend's big-eared bats share one additional characteristic. As noted in chapter 3 (see "Breeding" and "Inter-Site Movement";

also see above, this chapter, "Anthropogenic Disturbance"), Townsend's big-eared bats will abandon a cave or cave analog where they experience almost any anthropogenic disturbance, and they may not return for years after. As a result, occupied caves and cave analogs tend to be sites with very low or no incidences of anthropogenic disturbance.

CHEMICAL CONTAMINANTS

Full name: **The concentrations of chemical contaminants in the air, on plant surfaces, and/or on the ground or in surface waters in and around existing or potential Townsend's big-eared bat roosting and foraging habitat**. This element includes chemicals that may contaminate arthropods on which Townsend's big-eared bats feed or surface waters where the bats may drink. In principal, such contaminants includes biocides, mineral (e.g., metal, acid) leachates, and industrial wastes. As noted in chapter 3 (see "Chemical Stress"), Townsend's big-eared bats in one or more life stages are vulnerable or thought to be vulnerable to chemical stress from several types of contaminants, including:

- Soluble metals and mining industrial wastes due to roosting in abandoned underground mines, including in contaminated waters within or associated with such underground mines (Gruver and Keinath 2006; O'Shea et al. 2018). Some metals may bioaccumulate in Townsend's big-eared bat body tissues (Gruver and Keinath 2006).

- Pesticides, including organochlorine compounds, to which the bats are exposed indirectly through their ingestion of arthropods directly exposed to these compounds. These compounds and their breakdown products can bioaccumulate in the bats (Gruver and Keinath 2006). As noted in chapter 3 (see "Chemical Stress"), Townsend's big-eared bats do not appear to forage actively over agricultural areas where pesticides may be used to control insects (see chapter 3, "Foraging"), but they do forage around the edges of such areas. Further, aerial spraying of pesticides can result in contamination of adjacent, non-agricultural areas where the species may forage.

  Townsend's big-eared bat pups appear to be particularly susceptible to the bioaccumulation of fat-soluble contaminants from their mothers' milk, and these body loads persist as the individuals mature, potentially resulting in reproductive impairment or failure (Gruver and Keinath 2006). As recently emphasized by the European Food Safety Authority (Hernández-Jerez et al. 2019), pesticide exposure poses a risk to all insectivorous bats worldwide.

- Radon, which the bats may absorb when roosting in caves and abandoned uranium mines, "…but the health effects of such exposure remain unknown" (O'Shea et al. 2018).

The literature reviewed for this CEM does not explicitly identify any particular chemical contaminants of concern for Townsend's big-eared bats or their food resources along the Lower Colorado River Valley. A full review of the potential literature on chemical contaminants that could affect Townsend's big-eared bats or their food resources in the valley is beyond the scope of this CEM.

FIRE REGIME

Full name: **The frequency, timing, spatial extent, and intensity of fire in and around existing or potential Townsend's big-eared bat roosting and foraging habitat**. Wildfires, fires set to manage vegetation and risks of wildfire (prescribed fires), campfires, and fires caused by human negligence or malice may affect Townsend's big-eared bats in any of four settings: (1) when fires occur in the vegetation patches where the species forages, (2) when fires burn hollow trees and buildings that the bats may use as night roosting sites, (3) when the fires burn the vegetation surrounding the entrances to caves and cave analogs, and (4) when people light fires in caves or cave analogs. As noted by Gruver and Keinath (2006), "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." Smoke and noise from fires may disturb the bats in caves and cave analogs even when the fire does not burn a part of the cave or cave analog where the bats are present.

Wildfire is a natural type of disturbance in the plant communities across the geographic range of the Townsend's big-eared bat, including the Lower Colorado River Valley, and wildfires today also occur through human accidents and arson (Conway et al. 2010; LCR MSCP 2014; Meyer 2005; Steel et al. 2018; Stromberg et al. 2009). The LCR MSCP sometimes uses prescribed fire as a tool for habitat management (LCR MSCP 2014). Wonkka et al. (2018) provide a recent review of the literature on the effects of fire on riparian communities containing both plains cottonwood (*Populus deltoides monilifera*) and saltcedar (specifically *Tamarix ramosissima*) in the Western United States; Steel et al. (2018) provide a recent review of the effects of wildfire on bat occupancy in the Sierra Nevada in California.

Fire can affect Townsend's big-eared bat foraging habitat along the LCR by facilitating the replacement of large cottonwood trees by arrowweed (*Tessaria sericea*) and non-native species such as saltcedar (Busch 1995). For example, a fire at the Cibola National Wildlife Refuge-Island Unit in August 2011 burned cottonwood-willow vegetation that may have provided preferred foraging habitat

for Townsend's big-eared bats (Mixan and Diamond 2017b) (see below, this chapter, "Tree and Shrub Vegetation"). The species is frequently detected during acoustic monitoring at the refuge. Fire can also damage fixed acoustic monitoring stations (Mixan et al. 2013) or create openings useful for placing mist nets (Hill 2018).

INFECTIOUS AGENTS

Full name: **The species, abundances, spatial and temporal distributions, and activity levels of infectious agents that may affect Townsend's big-eared bats**. Townsend's big-eared bats in every life stage presumably are vulnerable to infection, as are all animals. Infectious agents include viruses, bacteria, fungi, and parasites. Non-lethal infections may make the affected individuals vulnerable to mortality from other causes.

As noted in chapter 3 (see "Disease"), Townsend's big-eared bats may host the rabies virus (Stuchin et al. 2018). However, the literature reviewed for this CEM does not document the incidence of illness in Townsend's big-eared bats due to a rabies infection (Gruver and Keinath 2006; O'Shea et al. 2018). Gruver and Keinath (2006) mention one study that found Townsend's big-eared bats hosting two species of fleas (*Nycteridopsylla vancouverensis* and *Myodopsylla palposa*), but with unknown effects. As mentioned in chapter 3 (see "Disease"), O'Shea et al. (2018) identify several studies that found ectoparasites and endoparasites in Townsend's big-eared bats, but without evidence of associated mortality. O'Shea et al. (2018) also note that, so far, the Townsend's big-eared bat has encountered the white-nose fungal syndrome across the entire range of its eastern subspecies and as far west as western Oklahoma and Texas without evidence of deleterious disease effects; otherwise, there appears to be little published work on infectious agent loads among Townsend's big-eared bats.

MATERNAL CARE

Full name: **The frequency, quantity, and quality of maternal care—nursing, cleaning, guarding, and thermoregulation—provided by reproductive female Townsend's big-eared bats to their pups prior to weaning**. As discussed in chapter 3 (see "Maternal Care"), adult females engage in maternal care of their single pups as a critical biological activity or process. In turn, pups experience maternal care as a habitat element. The description of maternal care as a critical biological activity or process for adult females in chapter 3 also describes maternal care as a habitat element for Townsend's big-eared bat pups.

MONITORING, CAPTURE, HANDLING

Full name: **The methods, frequencies, timing, and duration of (a) monitoring of Townsend's big-eared bat habitat and (b) monitoring, capture, and handling of Townsend's big-eared bats during field investigations**. Including this habitat element in the CEM makes it possible to address two topics: (1) the potential ways in which monitoring, capture, and handling can affect Townsend's big-eared bats, for example by causing mechanical stress, and (2) the potential ways in which Townsend's big-eared bat behaviors, such as foraging and roosting behaviors, can affect the ability of different methods to detect the bats and affect decisions about monitoring practices.

Bats have unique sensitivities to, and face unique risks of stress and injury from monitoring, capture, and handling (Greenhall and Paradiso 1968). As summarized, for example, by O'Shea et al. (2004), Ellison et al. (2013), the National Park Service (NPS Institutional Animal Care & Use Committee 2016), and Sikes et al. (2016):

- Disturbance of roosting bats during the cold season can deplete their fat stores, increasing their vulnerability to other threats.

- Manual capture of roosting bats and capture of flying bats in mist nets and traps can result in stress and injuries when the bats encounter the equipment and as they struggle to free themselves.

- Handling of bats to collect measurements and tissue samples and to attach identification and tracking devices can result in further stress and injuries.

- The identification and tracking devices can themselves cause harm. Some types of banding in particular can cause significant, debilitating injuries and, therefore, are now considered unacceptable (see also Bat World Sanctuary 2010).

However, most field studies do not collect systematic data on the types and rates of stress and injuries to bats associated with different types and steps in monitoring, handling, and tracking. Systematic investigations of such interactions mostly are limited to studies designed exclusively for that purpose (e.g., Ellison et al. 2007). Byrne et al. (2015) propose a methodology for increasing the recording of data on stress and injuries during field studies, to improve the adaptive management of bat monitoring. Spotswood et al. (2011) make a similar argument for tracking the effects of mist netting of birds.

The monitoring of bats in the Lower Colorado River Valley, including Townsend's big-eared bats, has long followed clear protocols for all monitoring practices, with routine reporting of protocols and their refinements (Berry et al.

2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Brown 2006, 2010, 2013; Calvert 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Hill 2018; LCR MSCP 2008; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2012, 2013; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010). These protocols cover visual surveys, mist netting and harp trapping, the use of banding and radio tracking devices, tissue sampling, and acoustic monitoring and the digital processing of acoustic recordings. The protocols explicitly recognize and address needs to: (1) minimize stress and harm to bats captured in mist nets and handled after capture; (2) raise mist nets at specific times of the night to ensure they capture bats not as they leave their roosts but instead later during foraging; (3) use harp traps instead of mist nets under some circumstances (see chapter 3, "Mechanical Stress"); and (4) begin acoustic recording before sunset and end it after sunrise, to ensure complete coverage of bat foraging activity. The protocols also identify times of the night when bats are inactive and field teams with mobile acoustic monitoring equipment therefore need not conduct monitoring (Hill 2018). However, the bat monitoring protocols in use in the Lower Colorado River Valley do not include the systematic recording of data on stress or injuries. As a result, it is not possible to estimate the effectiveness of the protocols for minimizing injury or stress.

The protocols for monitoring of bats in the Lower Colorado River Valley also require that radio tracking devices be attached only to larger individuals (weighing more than 10 grams) that can carry a device without stress (Mixan et al. 2015). The rate of growth of juvenile Townsend's big-eared bats (i.e., the rate at which they achieve adult size) affects the availability of juveniles large enough for the attachment of a tracking device. Finally, the protocols call for extreme caution when entering caves or other cave analogs where Townsend's big-eared bats may be roosting in order to avoid disturbing the bats or, in the extreme, causing them to abandon the site.

Conversely, the concentration of Townsend's big-eared bats at the entrances to roosting caves or cave analogs when leaving from or returning to their roosts, and their affinity for foraging and/or commuting to foraging areas along the edges of vegetation patches, both affect decisions on where to place netting or trapping devices. Similarly, the relatively low amplitude of Townsend's big-eared bat echolocation calls affects the likelihood of their detection by acoustic monitoring, depending on the design and placement of the detector (see chapter 3, "Foraging").

TEMPERATURE

Full name: **The mean air temperature in and around existing or potential Townsend's big-eared bats roosting and foraging habitat**. This element refers to the average air temperature both within and outside individual caves or

cave analogs that offer potential roosting locations for the species. Different locations within a cave or cave analog can have different air temperature regimes (i.e., different patterns of variation in temperature over time) depending on how air from the ground surface circulates through the system and whether the system has geothermal features or connections. The bats also can affect the air temperature locally within a cave or cave analog by aggregating in self-insulating, thermally self-regulating clusters. Outside air temperatures, in turn, vary with the weather, season, altitude, and climate.

The large geographic range of Townsend's big-eared bats indicates that average outside temperatures place only broad constraints on species distribution. As noted in chapter 1, the overall range of the Pacific subspecies, *C. T. townsendii*, extends north to south from southern British Columbia, Canada, to northern Sonora, Mexico; west-to-east from the Pacific coast to southern Montana, western South Dakota, western Colorado, and western New Mexico; and from sea level to 2,400 m (7,900 feet) elevation (AZGFD 2003; Piaggio et al. 2009).

As also noted in chapter 1, the major seasonal movements of Townsend's big-eared bats from cold- to warm-season roosts, and vice versa, appear to occur at roughly the same times everywhere across this large geographic range regardless of latitude, altitude, or ecological setting. This rough synchronicity suggests that photoperiod and/or relative (but not absolute) seasonal changes in ambient air temperature at least partially constrain the timings of these major movements; however, the bats select cold- and warm-season roosting locations in the interiors of caves and cave analogs with total to near-total darkness and relative stable temperatures (see immediately below). As a result, they must be sensitive to very small changes in light or temperature while roosting, and/or their major seasonal movements must be conditioned by other types of cues or internal biological processes as well. As noted by Gruver and Keinath (2006), the movement of Townsend's big-eared bats to hibernacula also "… may require northward or elevational migration to find roosts with suitable temperatures for hibernation (Pierson et al. 1999)."

The LCR MSCP (2016) notes the following concerning Townsend's big-eared bat behaviors and the locations where they prefer to roost within caves and cave analogs during the cold season:

> *In early winter, they may roost near the entrance, but if temperatures drop below freezing, they will move into deeper, more stable parts of the cave or mine (Kunz and Martin 1982). When hibernating, [they] are known to cluster and curl their ears when the temperature drops. Females have been found to inhabit colder winter sites than males (Pearson et al. 1952). In the West,[they] select roosts with cold, stable temperatures and moderate airflow (Humphrey and Kunz 1976; Kunz and Martin 1982). Temperatures have been found to range from -2.0–13.0 °C, with temperatures below 10 °C preferred (Pearson et al. 1952; Twente 1955; Humphrey and Kunz 1976; Pierson and Rainey 1998).*

Gruver and Keinath (2006) summarize Townsend's big-eared bat temperature affinities for warm-season roosting locations within caves and cave analogs as follows:

> *Internal temperature, which dictates energy expenditure by bats, appears to drive the selection of maternity roosts. ... maternity roosts of* Corynorhinus townsendii *in California ranged between 18 and 30 ºC (64 and 86 ºF) and were significantly 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 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.*

As noted above, this chapter (see "Caves and Cave Analogs"), Townsend's big-eared bats in both the cold and warm seasons may prefer caves and cave analogs for roosting with greater structural complexity and smaller openings. As summarized by Gruver and Keinath (2006), greater internal complexity and dimensions in a cave or cave analog likely results in "… 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)." Further, smaller cave and underground mine openings result in more stable temperature and humidity profiles within the structures by constraining air exchange between the ground surface and the interior. Presumably, gates across cave or underground mine openings, and dense vegetation around these openings, also may constrain such air exchange.

TREE AND SHRUB VEGETATION

Full name: **The taxonomic composition and density, vertical and horizontal structure, patch size and spatial distribution, and maturity and temporal dynamics of tree and shrub vegetation in and around existing or potential Townsend's big-eared bat foraging habitat and around the entrances to existing or potential roosting sites**. As noted in the "Definitions" section immediately following the "Acronyms and Abbreviations" at the beginning of this report, this CEM recognizes plant communities along the Lower Colorado River Valley as consisting of canopy, understory, shrub, and herbaceous layers. Trees, that is, woody vegetation greater than 2.0 meters in height, make up the

canopy layer and may also occur in the understory as subcanopy trees. Where trees are absent, shrubs comprise the uppermost layer of vegetation; where trees are present, shrubs and herbaceous plants make up the understory.

As indicated in the full name of this habitat element, Townsend's big-eared bats appear to be affected by the tree and shrub vegetation in their environments in two general ways. First, tree and shrub vegetation affects their foraging, including their commuting between roosting sites and foraging areas. Second, it affects conditions around the entrances to their roosting sites. In contrast, Gruver and Keinath (2006) found that:

> *Throughout its western range,* Corynorhinus townsendii *roosts in a variety of vegetative communities, and at a range of elevations … 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.*

Gruver and Keinath (2006) specifically found in their review of the literature that Townsend's big-eared bats roost in landscapes dominated by saxicoline brush, sagebrush, semidesert scrub, pinyon-juniper woodland, ponderosa pine woodland, montane forest, and subalpine forest in Colorado; by Mohave and Great Basin desert scrub, pinyon-juniper woodland, and bristlecone-limber pine forest in the White and Inyo Mountains of California and Nevada (*aka* Inyo-White Mountains; Anderson et al. 2018); by desert scrub, oak woodlands, oak-pine forests, pinyon-juniper forests, and coniferous forests in Arizona; by sagebrush-grass steppe, juniper woodlands, and mountain brush in Utah; and by coastal lowlands, cultivated valleys, and hills with mixed vegetation in central California and Washington.

Gruver and Keinath (2006) further state:

> *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.*

As noted in chapter 3 (see "Foraging"), riparian edges near surface water may offer especially abundant insect populations for foraging as a result of aquatic insect productivity (Blakey et al. 2017; Hagen and Sabo 2012, 2014; Rubin et al. 2014;). They also generally avoid highly developed areas. As also noted in chapter 3 (see "Foraging"), the affinity of the species for foraging along the edges of openings and corridors in taller vegetation affects the likelihood of their capture in mist nets placed in such settings versus in more homogeneous vegetation settings (Calvert 2010a, 2010b, 2014, 2016a, 2016b; Hill 2018; LCR MSCP 2008).

Limited data from the Lower Colorado River Valley help refine this overall picture of vegetation associations for foraging. Vizcarra (2011) and Vizcarra and Chambers (2011) studied Townsend's big-eared bat foraging habitat preferences in the valley in 2008–10 based on nocturnal acoustic detections across different vegetation types at 72 sampling locations. The acoustic monitoring stations were located specifically in areas with four broad vegetation types, labeled as "cottonwood/willow," "mesquite" (saltcedar/honey mesquite [*Prosopis glandulosa*] and saltcedar/screwbean mesquite [*P. pubescens*]), "saltcedar," and "marsh." Locations were selected based on a previous digital classification of vegetation types from aerial photographs taken in 2004 (BIO-WEST, Inc., and GEO/Graphics, Inc. 2006), updated to incorporate recent restoration areas. For Townsend's big-eared bats, Vizcarra specifically assessed the relative percentage of the area within 100 m of each station dominated by each vegetation type, for comparisons against acoustic detection frequency, with the results expressed in the form of a predictive occupancy model. The study included all maturity classes for the four vegetation types but did not examine the effects of variation in the density or maturity of the vegetation within these types.

The results obtained by Vizcarra (2011) (also see Vizcarra and Chambers 2011) (i.e., the predictive occupancy model for Townsend's big-eared bat foraging habitat preferences based on her acoustic monitoring data) indicate that the species is more likely to forage in cottonwood-willow vegetation regardless of the relative percentage of the area within 100 m (328 feet) of each acoustic monitoring station dominated by this vegetation type; less likely to forage in areas of mesquite-dominated vegetation or marsh, the greater the relative percentage of area they cover; and more likely to forage in areas of saltcedar dominated vegetation, the greater the relative percentage of area it covers. This plasticity fits the predictions summarized by Gruver and Keinath (2006), quoted immediately above. Vizcarra (2011) also notes:

> *The relationship with saltcedar is somewhat puzzling, considering that this species is known to be a moth specialist (Burford and Lacki 1998), which are conspicuously lacking in saltcedar habitats (Anderson et al. 2004). Saltcedar hosts an abundance of other insect taxa, such as leafhoppers (Homoptera: Cicadellidae), which have been found to be important in the diets of other species of bats (Whitaker 1995, 1996; Sparks and Valdez 2003, O'Farrell et al. 2004).*

> *Townsend's big-eared bats are sufficiently flexible in their diet to take advantage of available prey, and could be foraging on leafhoppers associated with saltcedar … The use of mature saltcedar could be explained by their selection of cluttered microhabitats (O'Farrell and Gannon 1999), which is a characteristic of mature saltcedar stands.*

The finding by Vizcarra (2011) concerning saltcedar also contradicts the perception that the Townsend's big-eared bat avoids foraging in areas of non-native vegetation (Maturango Museum and Brown-Berry Biological Consulting 2018).

The literature review by Gruver and Keinath (2006) further found that western Townsend's big-eared bats avoid foraging in either dense forest or over open grasslands, preferring vegetation with a mosaic of trees, shrubs, and open areas of herbaceous cover and, therefore, a mixture of vegetation with edges (vertical faces) at a range of heights. For example, they report:

> *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).*

As noted in chapter 3 (see "Foraging"), only eight Townsend's big-eared bats have been tracked along the Lower Colorado River Valley, all from Gold Dollar Mine in August 2016, resulting in very limited data on vegetation associations during foraging (Maturango Museum and Brown-Berry Biological Consulting 2018). The tracking data (Maturango Museum and Brown-Berry Biological Consulting 2018) indicate that:

> *The movement after roost emergence was directed to the northeast and east in a broader fan toward the LCR…. The foraging habitat varied between native vegetation along the LCR and remnant oxbows of the historic LCR near Poston, to planted trees (possibly cottonwoods) associated with buildings on CRIT land. Because the ground trackers could not leave paved roads, foraging habitat on CRIT land was not precisely determined. Individual bats exhibited foraging area fidelity … and made regular stops to night roost in several buildings on CRIT.*

The August 2016 telemetry data are not sufficiently detailed to evaluate whether the tracked bats moved more along edges of taller vegetation versus open areas during foraging or commuting to and from foraging areas. As noted in chapter 3 (see "Foraging"), Fellers and Pierson (2002) demonstrate the level of spatial precision required and a suitable sampling design for obtaining data on the details of Townsend's big-eared bat foraging navigation.

Tree and shrub vegetation potentially may affect Townsend's big-eared bats indirectly by affecting the compositions, abundances, and spatial and temporal

distributions of arthropod and vertebrate communities across the landscape (see above, this chapter, "Arthropod community" and below, "Vertebrate Community"). These factors, in turn, affect foraging opportunities for the bats and the risks of predation. The latter may be particularly important around the entrances to the caves and cave analogs where the bats roost. As noted in chapter 3 (see "Predation"), the density of vegetation around the entrances may affect the types of predators that may forage at these locations and their likelihood of success in capturing the bats as the enter or leave.

VERTEBRATE COMMUNITY

Full name: **The taxonomic, functional, and size composition; abundance; activity levels; and temporal dynamics of the community of vertebrates—birds, mammals, reptiles, and amphibians—that may occur in or around existing or potential Townsend's big-eared bat roosting and foraging habitat**. This element refers to the range of vertebrate species known or suspected to interact with Townsend's big-eared bats or its habitat along the Lower Colorado River Valley, particularly as competitors, predators, or ecosystem engineers.

The literature provides only scattered information on the vertebrate species that may prey on Townsend's big-eared bats in the Lower Colorado River Valley or elsewhere. The subject remains largely unstudied; however, the few available studies, along with reviews of predation on bats in general (Mikula 2015; Mikula et al. 2016), provide some guidance. As noted in chapter 3 (see "Predation"), Townsend's big-eared bats are vulnerable to predation in four settings: (1) in their seasonal and interim (transient) roosts within caves, underground mines, crevices, and overhangs, (2) as the bats exit and enter the openings of caves and underground mines, (3) from the air during foraging and inter-site movement, and (4) from the ground, when their foraging activities bring them close to the ground. Further, because Townsend's big-eared bats forage and travel only at night, their vulnerability to predation in the latter three settings occurs only at night, when owls, in particular, are most active.

Owls that potentially could prey on Townsend's big-eared bats at night along the Lower Colorado River Valley include the barn owl (*Tyto alba*), ferruginous pygmy-owl (*Glaucidium brasilianum*), great horned owl (*Bubo virginianus*), and western screech-owl (*Otus kennicottii*) (Arizona-Sonora Desert Museum 2019). However, the subject of owl predation on Townsend's big-eared bats has not been studied. Gruver and Keinath (2006) note, "Although several reports have documented the presence of bat remains in owl pellets …, 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."

Gruver and Keinath (2006) summarize other reports of predation on Townsend's big-eared bats as follows:

> *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* [Felis catus] *and raccoons* [Procyon lotor] *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.*

Other potential vertebrate predators on Townsend's big-eared bats specifically mentioned in the literature (LCR MSCP 2016) that occur in the Lower Colorado River Valley include Western spotted skunks (*Spilogale gracilis*) and ringtails (*Bassariscus astutus*). The native Sonoran lyresnake (*Trimorphodon lambda*) and/or nearly identical and possibly conspecific California lyresnake (*T. lyrophanes*) (Brennan 2008), a climbing snake known to prey on roosting bats (Esbérard and Vrcibradic 2007)[3], also occur(s) in the greater Lower Colorado River Valley: An individual photographed in the Planet Ranch section of the lower Bill Williams River valley in 2014 was recently confirmed as *T. lambda* (Hill 2019, personal communication). Elliott et al. (2017) mention a report of a California lyresnake with a bat (*Myotis velifer*) wedged in its throat in a mine in the Riverside Mountains in California. Townsend's big-eared bats historically roosted in abandoned underground mines in these mountains and continue to do so today, from which locations they forage across the Lower Colorado River Valley (see chapter 3, "Foraging"; also see above, this chapter, "Caves and Cave Analogs").

Theoretically, as noted in the discussion of competition in chapter 3, other bats and other insectivorous vertebrates may compete with Townsend's big-eared bats for food or roosting sites; however, as also noted in chapter 3, the literature reviewed for this CEM provides no information on such competition. Townsend's big-eared bats appear to partition food and roosting resources efficiently with other bat species.

The literature does identify at least three vertebrates that may affect Townsend's big-eared bats indirectly by modifying their potential foraging habitat. Beavers (*Castor canadensis*) can alter riparian vegetation communities in the Southwestern United States by removing cottonwood and willow. As quoted from Gruver and Keinath (2006) in this chapter, "Tree and Shrub Vegetation":

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[3] Esbérard and Vrcibradic (2007) specifically address *T. biscutatus*, the western lyresnake, of which the Sonoran lyresnake was until recently considered a subspecies.

> *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.*

Beavers were once common in the LCR ecosystem (Grinnell 1914; Minckley and Rinne 1985; Ohmart et al. 1988) and are increasingly active there again today (Hautzinger 2010; Mueller 2006; Shafroth and Beauchamp 2006; Vizcarra and Piest 2010). Beaver activity may alter riparian vegetation communities in other ways as well. Their activity along one section of the Bill Williams River has "… maintain[ed] fluctuating water levels and pathways, which has limited colonization of saltcedar and promoted growth of native wetland vegetation" (Cotten and Grandmaison (2013) while simultaneously favoring colonization of saltcedar immediately around such inundated areas (Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b).

Grazing by mule deer (*Odocoileus hemionus*) and non-native cattle (Bovidae) and burros (*Equus asinus*) across the arid Southwestern United States, in turn, can degrade riparian habitat. For example, grazing may thin the understory or prevent the establishment of cottonwood and willow seedlings (Kauffman et al. 1997). Krueper (1993) and Krueper et al. (2003) report that fencing cattle out of sensitive riparian habitats in the San Pedro Riparian National Conservation Area in southeastern Arizona led to improved habitat quality and increased riparian bird density within 4 years.

WATER AVAILABILITY

Full name: **The spatial and temporal availability of surface water, including small pools in and around existing or potential Townsend's big-eared bat roosting and foraging habitat, and the depth of the water table in these settings**. This element refers to the presence of surface water near foraging areas or roost sites. As noted in chapter 3 (see "Chemical Stress"), Townsend's big-eared bat juveniles and adults appear to obtain most or all of their water by drinking directly from surface water bodies. Gruver and Keinath (2006) note that they drink specifically "… by skimming the surface of calm water bodies, and they appear to avoid open water with too much clutter (i.e., vegetation)." As a result, Townsend's big-eared bat juveniles and adults require the presence (within a suitable travel distance) of surface water bodies large enough for skimming. The LCR MSCP (2016) specifically notes that the bats prefer sites for their maternity roosts with "… distance to water of within 100 m for coastal populations and 8,000 m for others." Nelson and Gillam (2019) detected Townsend's big-eared bats foraging at sites located within 250 m of water, among a sample of sites in North Dakota, and note that the species foraged at sites

located farther from water than did most other bat species in their study area. Townsend's big-eared bat pups, in contrast to adults, obtain all of their water through nursing.

Water availability potentially may affect Townsend's big-eared bats indirectly by affecting the arthropod and vertebrate communities and tree and shrub vegetation across the landscape around their roosting sites (see above, this chapter). For example, a general lowering of water tables in the Southwestern United States has been linked to changes in the riparian vegetation community, with declines in cottonwood and willow species and increases in saltcedar (Stromberg 1998).

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics, both natural and anthropogenic, that affect the abundance, spatial and temporal distributions, and quality of habitat elements. Controlling factors may also significantly directly affect some critical biological activities or processes. Table 4 lists the eight controlling factors included in this CEM and the habitat elements they directly affect. Controlling factors may affect each other and may indirectly affect other habitat elements through their effects on other controlling factors or through the cascading effects of habitat elements on each other.

Table 4.—Proposed controlling factors affecting Townsend's big-eared bats in the LCR ecosystem and the habitat elements they directly affect

(Xs indicate the habitat elements that affect each critical biological activity or process. The table does not show two habitat elements—maternal care and temperature—that are not directly affected by any controlling factor.)

Habitat element ➔ / Controlling factor ⬇	Anthropogenic disturbance	Arthropod community	Caves and cave analogs	Chemical contaminants	Fire regime	Infectious agents	Monitoring, capture, handling	Tree and shrub vegetation	Vertebrate community	Water availability
Conservation monitoring and research programs							X			
Fire management					X					
Habitat development and management	X							X		
Mining and mine management	X		X	X						X
Nuisance species introduction and management		X		X	X	X		X	X	
Recreational use of caves and abandoned mines	X				X					
Surrounding land use	X	X		X				X	X	
Water storage-delivery system design and operation										X

A hierarchy of controlling factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on eight immediate controlling factors that are within the scope of potential human manipulation, particularly manipulation by the LCR MSCP and its conservation partners.

The eight controlling factors identified in this CEM do not constitute individual variables; rather, each identifies a category of variables (including human activities) that share specific features that make it useful to treat them together. In particular, each controlling factor covers activities with similar effects or management implications across multiple life stages and across multiple species of concern to the LCR MSCP. Categorizing such activities together across multiple species and multiple life stages of these species makes it easier to compare and integrate the CEMs across the LCR MSCP.

CONSERVATION MONITORING AND RESEARCH PROGRAMS

Full Name: **The types, frequencies, and duration of monitoring and research activities carried out by the LCR MSCP, other Federal agencies, States, and Tribes focused on species and habitats of concern to their respective wildlife conservation programs**. The HCP (Reclamation 2004) for the LCR MSCP directs the program to carry out conservation measures to meet the biological needs of 5 threatened or endangered species and 19 other covered species and to potentially benefit 5 evaluation species. The Townsend's big-eared bat is an evaluation species. The LCR MSCP carries out many of these conservation measures in partnership with other agencies. The conservation measures include monitoring of species distributions as well as several types of research investigations. The current LCR MSCP annual work plan and 5-year monitoring and research priorities specifically call for field-based research investigations to characterize habitat requirements and habitat conditions, including conditions at created and managed habitat sites, for 22 species, including Townsend's big-eared bats (LCR MSCP 2018a, 2018b).

FIRE MANAGEMENT

Full name: **The types, frequencies, and duration of activities intended to control and/or suppress fire in and around existing or potential Townsend's big-eared bat roosting and foraging habitat and across lands surrounding these locations**. The LCR MSCP and other land management agencies along the LCR and Bill Williams River valleys may use prescribed fire as a management tool and actively manage wildfires through fire suppression and the construction of fire control breaks (LCR MSCP 2018a). Wildfire is a natural type of disturbance in the riparian plant communities of the Lower Colorado River Valley, and wildfires today also occur through human accidents (Conway et al. 2010; LCR MSCP 2018a). In fact, wildfires have occurred recently at LCR MSCP restoration sites (Hunters Hole and Yuma East Wetlands) and in riparian

habitat at the Havasu National Wildlife Refuge and Cibola National Wildlife Refuge-Island Unit (Hill 2018; J. Hill and C. Ronning 2018, joint personal communication; LCR MSCP 2018a).

HABITAT DEVELOPMENT AND MANAGEMENT

Full name: **The types, frequencies, and durations of actions taken by the LCR MCP to create and manage habitat for species conservation in and around existing or potential Townsend's big-eared bat foraging habitat, including actions to affect the taxonomic composition, abundance, condition, and spatial distribution of vegetation**. The HCP (Reclamation 2004) directs the LCR MSCP to carry out conservation measures to meet the biological needs of 5 threatened or endangered species and 19 other covered species and to potentially benefit 5 evaluation species. These measures include creating and managing habitat to meet these biological needs through the manipulation particularly of vegetation and hydrology. The LCR MSCP and other land managers along the LCR and Bill Williams River valleys use a range of methods to establish and manage the vegetation (see chapter 4, "Tree and Shrub Vegetation") on lands under their authorities, including prescribed fire, surface irrigation and subirrigation, planting, fertilizing, thinning and hand removal, discing and plowing, and the application of herbicides (LCR MSCP 2014, 2018a; Reclamation 2004). Agencies and irrigation and drainage districts may also remove vegetation to maintain roads and canals under their authorities.

As noted in chapter 1, Townsend's big-eared bats historically maintained and currently maintain both cold- and warm-season roosts within the Lower Colorado River Valley but only outside the boundaries of the LCR MSCP planning area (Berry et al. 2017; Brown 2006, 2010, 2013; LCR MSCP 2016; Maturango Museum and Brown-Berry Biological Consulting 2018). At the same time, the species forages heavily within the planning area, commuting from its daytime roosts to foraging habitat within the planning area. The LCR MSCP therefore recognizes the Townsend's big-eared bats that use the planning area as an LCR population. Consequently, this CEM addresses the overall landscape used by the species along the valley, not just the portions that lie within the LCR MSCP planning area. However, the CEM recognizes that habitat development and management activities by the LCR MSCP and other land managers along the LCR and Bill Williams River valleys do not affect Townsend's big-eared bat daytime roosting habitat; instead, they affect Townsend's big-eared bat foraging habitat and the landscape through which the species commutes during foraging excursions from its daytime roosts outside the LCR MSCP planning area to foraging habitat within that area.

MINING AND MINE MANAGEMENT

Full name: **The design, construction, and operation of underground mines, and the management of inactive underground on lands surrounding the LCR MSCP planning area**. The uplands surrounding the LCR and Bill Williams River historic floodplains have long histories of underground mining. As summarized by Randall et al. (2010), mining began in the region in 1849 following the discovery of gold at the foot of the Avawatz Mountains. Mines have extracted "… not only gold, but also silver, lead, copper, iron, molybdenum, lead, tungsten, zinc, borates, talc, and other materials from the region." Numerous active and inactive underground mines occur in the uplands surrounding the Lower Colorado River Valley in Arizona, California, and Nevada. Inactive mining sites around the valley include many sites abandoned by their former operators and consequently now managed by public land management agencies such as the Federal Bureau of Land Management or one of the three States along the LCR.

The design, construction, and operation of underground mines includes activities associated with ore processing; the transportation of equipment, mining wastes, and ore processing wastes; mitigation of hazards associated with such operations; and controlling public access to the underground mines and surrounding industrial areas. The management of inactive underground mines may include activities to mitigate physical and chemical hazards to people and wildlife that may enter the abandoned underground mine or its surroundings, an inactive industrial area, or activities associated with controlling public access to the mine interior. Public access to the interiors of abandoned underground mines may result in accidental or intentional disturbance of bat colonies, fires, and injury to people. Land management agencies with responsibility for abandoned underground mine sites may install gates across mine entrances to prevent entry by unauthorized individuals while still allowing wildlife to pass (Brown 2006, 2010, 2013; Diamond and Diamond 2014).

The effects of mine entrance gating on Townsend's big-eared bats is a matter of debate. Diamond and Diamond (2014) studied the effects of gating on Townsend's big-eared bat flight behavior at maternity colonies in two previously gated (control) and two ungated (treatment) mines that were gated during this study. They found:

> *Overall circling activity increased more than 6-fold at openings of treatment mines following gating ($P < 0.001$). Crowding during emergence was significantly higher ($P = 0.023$) in newly gated mines than in previously gated mines. Gates affect subadults during the initial-volancy periods, as detected through collisions with the gates. Increased activity of bats and collisions with the gate, which result in bats falling to the ground at mine openings, may amplify vulnerability to predators and increase energetic demands.*

Tobin and Chambers (2017) reviewed the literature worldwide on the effects of gating on cave-obligate bats. They found that older gate designs (1950–70), such as cement walls or iron doors, consistently impaired bat use of caves and underground mines. In contrast, modern (1970s to present) gating designed to be compatible with bat activity had varying effects:

> *Short-term responses of bats to bat-compatible gates were negative and included increases in energetically expensive flight behaviors. Although long-term responses included a mix of population and species trends, we attribute these mixed responses in part to differences in flight agility among species. Bats with moderate to high agility (low wing loading, broad call bandwidths) adjust to gates, but species with proposed low agility (high wing loading and narrow call bandwidths) may abandon sites after gating. Other factors including bat density in roosts and size of the cave or mine entrance also affect acceptance of gates and should be considered in gate design.*

Sherwin et al. (2000a) also note that decisions whether or not to close individual abandoned mines can have significant effects on Townsend's big-eared bat site use across a locality. Their study found (see chapter 3, "Inter-Site Movement") that year-to-year variation in the use of different bachelor and maternity roosting sites can result in years when one or more individual sites may appear unused. They caution that single-year surveys to identify mines for possible closure—for public safety—may misidentify such temporarily unoccupied sites as "abandoned" by Townsend's big-eared bats. Gating such sites with barriers that completely block bat passage can then disrupt longer-term patterns of inter-site movement.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

Full name: **The introduction and management of nuisance species that potentially may interact with Townsend's big-eared bats in and around existing or potential Townsend's big-eared bat roosting and foraging habitat**. Nuisance species are non-native animals, plants, and micro-organisms that were not introduced and/or are not managed for recreational purposes. They may poison, infect, prey on, compete with, or present alternative food resources for native species; cause other alterations to the food web that affect native species; or affect habitat features such as vegetation cover. The factor includes the legacy of past introductions and the potential for additional introductions, and it includes both intentional and accidental introductions *other than* intentional introductions for recreation such as non-native fishes and game species. Management activities may include efforts to control the spread of nuisance species through interdiction and education, and through efforts to reduce the abundance and/or geographic range of species through mechanical removal, prescribed fire, applications of biocidal chemicals, and releases of biological controls. Agencies involved in nuisance

species management along the LCR and Bill Williams River valleys include the Bureau of Land Management, the State of Arizona, the U.S. Fish and Wildlife Service, Reclamation, Indian Tribes, and irrigation districts.

RECREATIONAL USE OF CAVES AND ABANDONED MINES

Full name: **The use of caves and abandoned underground mines on lands surrounding the LCR MSCP planning area as sites for recreational activities**. Some people enjoy exploring or simply spending time in caves and abandoned underground mines. As a result, caves and abandoned underground mines that provide, or potentially could provide, warm- or cold-season roosting sites for Townsend's big-eared bats attract recreational visitors as well. These visitors potentially can travel far enough into caves or underground mines to reach interior areas where Townsend's big-eared bats gather in maternal or bachelor colonies or in hibernacula. Noise, fires, or direct interference from the visitors can disturb the roosting bats, which may then flee and potentially abandon that cave or underground mine (Brown 2006, 2010, 2013). As noted above, this chapter (see "Mining and Mine Management"), land management agencies with responsibility for caves and abandoned underground mine sites may install gates across entrances to prevent entry by unauthorized individuals while still allowing wildlife to pass (Brown 2006, 2010, 2013).

SURROUNDING LAND USE

Full name: **The types and intensities of human activity on lands surrounding habitat conservation areas and other protected areas used or potentially usable by Townsend's big-eared bats as foraging habitat**. The lands surrounding LCR MSCP habitat conservation areas and other protected areas—particularly surrounding locations used or potentially usable by Townsend's big-eared bats as foraging areas—are subject to a wide range of uses. These uses include commercial and residential activities, irrigation farming, grazing, recreation, and multi-purpose range management. These uses frequently affect the taxonomic composition, abundance, condition, and spatial distribution of vegetation on these lands.

Irrigation farming specifically replaces native and otherwise uncontrolled vegetation with annual crops and orchards across many portions of the Lower Colorado River Valley. Farmlands are subject to surface irrigation and subirrigation, planting, fertilizing, thinning and hand removal, discing and plowing, and the application of herbicides and pesticides. Commercial and

residential areas also may be subject to irrigation and subirrigation, planting, fertilizing, vegetation thinning and pruning, and the application of herbicides and pesticides. All developed lands are also subject to intensive fire management.

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATION

Full name: **The design and operation of the water storage, diversion, and delivery system that regulates the elevation of surface water in and around existing or potential Townsend's big-eared bat foraging habitat**. This controlling factor specifically concerns the water storage-delivery system within the LCR MSCP planning area. The caves and underground mines potentially available to Townsend's big-eared bats as roosting sites in the greater Lower Colorado River Valley are all located in uplands away from the water storage-delivery system in the valley.

The Colorado River through the Lower Colorado River Valley consists of a chain of reservoirs separated by flowing reaches. The water moving through this system is highly regulated by Reclamation for storage and delivery to numerous international, Federal, State, Tribal, municipal, and agricultural holders of water rights, as well as for hydropower generation. The Bill Williams River below Alamo Dam similarly is regulated by the U.S. Army Corps of Engineers for flood control, recreation, water conservation, and wildlife conservation. This system of water management and its infrastructure, together with regulated discharges from the Upper Colorado River Basin and local weather conditions, determine surface water distributions and groundwater elevations along the LCR and Bill Williams River valleys, and deliveries of water to off-channel locations, including protected areas and habitat conservation areas (Reclamation 2004). River regulation and entrenchment of the LCR between the reservoirs have eliminated almost all opportunities for the river to deliver pulses of water onto its former floodplain and have altered water table elevations throughout the Lower Colorado River Valley. Reclamation, the U.S. Fish and Wildlife Service, and other agencies have rights to use some of the water in the LCR on lands managed as wildlife habitat, delivered through surface water diversions, and groundwater wells (LCR MSCP 2014, 2018a).

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains three sections, each presenting the CEM for a single life stage for Townsend's big-eared bats. Each section identifies the outcomes and critical biological activities and processes for that life stage, the habitat elements that determine the rates of these critical biological activities and processes, the controlling factors that determine the abundance, distribution, and other important qualities of these habitat elements; and the causal links among them.

The model for each life stage assesses the character and direction, magnitude, predictability, and scientific understanding of each causal link based on the following definitions (see attachment 1 for further details):

- **Character and direction** categorizes a causal relationship as positive, negative, or complex. "Positive" means that an increase in the causal node results in an increase in the affected node, while a decrease in the causal node results in a decrease in the affected node. "Negative" means that an increase in the causal node results in a decrease in the affected element, while a decrease in the causal node results in an increase in the affected node. Thus "positive" or "negative" here do not mean that a relationship is beneficial or detrimental. The terms instead provide information analogous to the sign of a correlation coefficient. "Complex" means that there is more going on than a simple positive or negative relationship. Positive and negative relationships are further categorized based on whether they involve any response threshold in which the causal agent must cross some value before producing an effect. In addition, the "character and direction" attribute categorizes a causal relationship as uni- or bi-directional. Bi-directional relationships involve a reciprocal relationship in which each node affects the other.

- **Magnitude** refers to "… the degree to which a linkage controls the outcome *relative to other drivers*" (DiGennaro et al. 2012). Magnitude takes into account the spatial and temporal scale of the causal relationship as well as the strength (intensity) of the relationship at any single place and time. The present methodology separately rates the intensity, spatial scale, and temporal scale of each link on a three-part scale from "Low" to "High" and assesses overall link magnitude by averaging the ratings for these three. If it is not possible to estimate the intensity, spatial scale, or temporal scale of a link, the subattribute is rated as "Unknown" and ignored in the averaging. If all three subattributes are "Unknown," however, the overall link magnitude is rated as "Unknown." Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link magnitude provide information analogous to the size of a correlation coefficient.

- **Predictability** refers to "… the degree to which current understanding of the system can be used to predict the role of the driver in influencing the outcome. Predictability … captures variability… [and recognizes that] effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult" (DiGennaro et al. 2012). A causal relationship may be unpredictable because of natural variability in the system or because its effects depend on the interaction of other factors with independent sources for their own variability. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link predictability provide information analogous to the size of the range of error for a correlation coefficient. The present methodology rates the predictability of each link on a three-part scale from "Low" to "High." If it is not possible to rate predictability due to a lack of information, then the link is given a rating of "Unknown" for predictability.

- **Understanding** refers to the degree of agreement represented in the scientific literature and among experts in understanding how each causal relationship works—its character, magnitude, and predictability. Link predictability and understanding are independent attributes. A link may be highly predictable but poorly understood or poorly predictable but well understood. The present methodology rates the state of scientific understanding of each link on a three-part scale from "Low" to "High."

Constructing the CEM for each life stage involves identifying, assembling, and rating each causal link one at a time. Analyses of the resulting information for each life stage can then help identify the causal relationships that most strongly support or limit life-stage outcomes, support or limit the rate of each critical biological activity or process, and support or limit the quality of each habitat element, as that element affects other habitat elements or affects critical biological activities or processes. Analyses also can help identify which, among these potentially high-impact relationships, are not well understood.

All potential causal links—among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes—affecting each life stage are recorded on a spreadsheet. This spreadsheet is then used to record information on the character and direction, magnitude, predictability, and scientific understanding for each causal link, along with the underlying rationale and citations, for each life stage. Software tools developed in association with these CEMs then allow users to generate a "master" diagram for each life stage from the data in the spreadsheet—or, more usefully, to query the CEM spreadsheet for each life stage and generate diagrams that selectively display query results concerning that life stage.

This CEM includes the master diagram for each life stage. The master diagrams display all causal links, of all character types and directions, magnitudes, predictabilities, and levels of understanding. The results can be visually complex but are included to give the reader an overall sense of the CEM for each life stage.

The master CEM diagram for each life stage shows the controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes for that life stage. The diagram displays information on the character and direction, magnitude, predictability, and scientific understanding of every link. The diagrams use a common set of conventions for identifying the controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes as well as for displaying information about the causal links. Figure 2 illustrates these conventions.

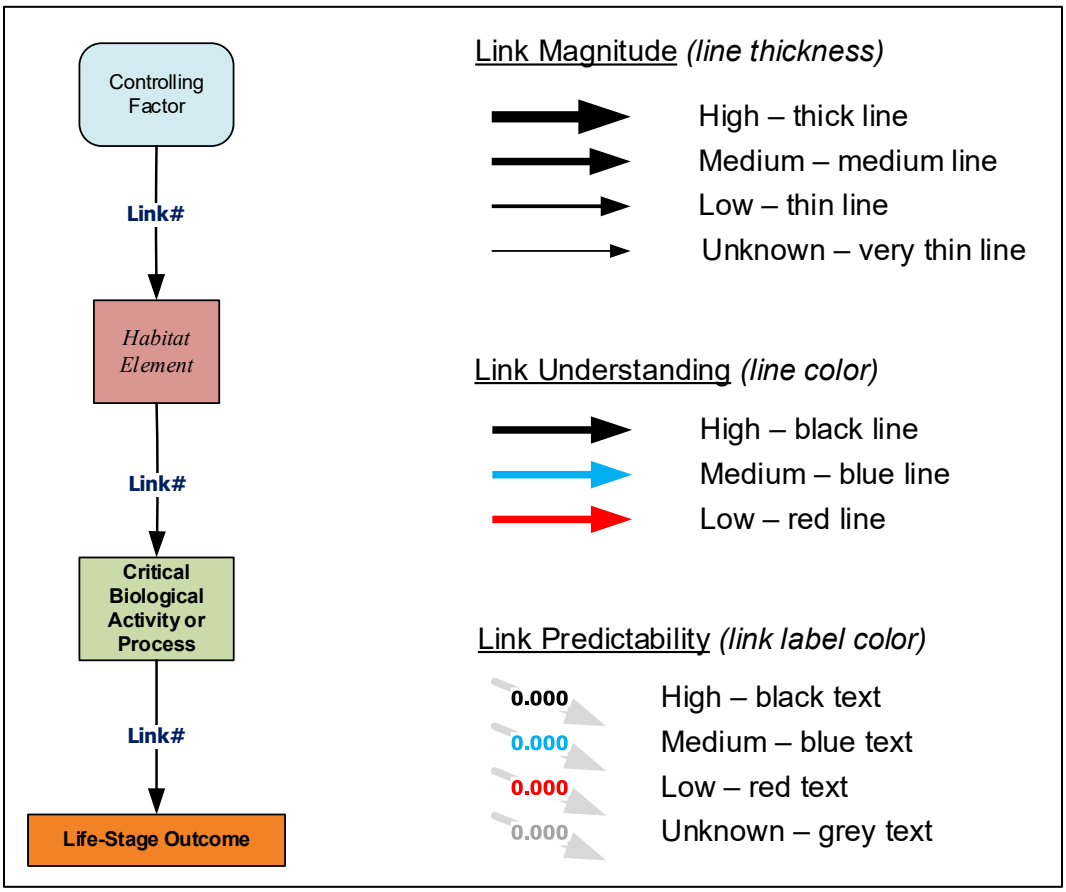

Figure 2.—Diagram conventions for LCR MSCP species conceptual ecological models.

The conventions for displaying information about the causal links are as follows: Links are represented by arrows, the point of which indicates the direction of causation. Bi-directional causal links are represented by arrows with points at both ends. The thickness of the arrow represents link magnitude, while the color

of the arrow represents link understanding. Each arrow has a label that uniquely identifies the link. The number to the left of the decimal place indicates the life stage (1…N), while the number to the right of the decimal place provides a unique index value for each link. The color of the label represents link predictability.

The discussions of each life stage in this chapter and of all three life stages considered together in chapter 7 include analyses of the information contained in the spreadsheet. The analyses highlight causal chains that strongly affect the outcomes for each life stage and identify important causal relationships with proposed high scientific uncertainty. The latter constitute topics of potential importance for investigation for adaptive management.

LIFE STAGE 1 – PUPS

As described in chapter 2, this life stage begins with the birth of a pup (maximum one per reproductive female adult per year) in its natal maternity colony sometime in March through April or later. The life stage ends when the pup is weaned. Pups are volant after 2.5 to 3 weeks but remain with their mothers and may continue nursing up to 6 weeks of age. This life stage has two life-stage outcomes (see figure 1): pup growth and pup survival. Schmidly and Bradley (2016) state that pups grow to nearly their full adult size by the time they are volant, suggesting a roughly fourfold increase in body mass during this life stage. Post-natal, pre-weaning survival is estimated to be 95 to 96 percent. Figure 3 (at the end of this section) presents the complete CEM for this life stage, showing all controlling factors, habitat elements, critical biological activities and processes, life-stage outcomes, and their linkages.

Much of what happens to Townsend's big-eared bat pups depends on the maternal care they receive, beginning with the selection of maternity roosting site itself (see chapter 3, "Maternal Care"). The CEM for the pup life stage therefore recognizes maternal care as a crucial habitat element for every pup; however, most of the dynamics that shape maternal care are addressed in the CEM for the adult life stage, presented later in this chapter.

The CEM proposes that pup growth affects pup survival but with unknown magnitude. As noted above (also see attachment 1), link magnitude refers to the degree to which a given component of the model controls some condition relative to other components affecting that same condition. Theoretically, faster maturation in Townsend's big-eared bat pups should convey lower vulnerability to threats specific to the pup life stage and, therefore, lead to a higher rate of survival. The relationship should be strong, based on core biological principles;

however, no studies have addressed the topic specifically for Townsend's big-eared bats or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is rated as low.

The CEM identifies seven critical biological activities or processes affecting one or both outcomes for this life stage: chemical stress, cold season: roosting, disease, feeding, mechanical stress, predation, and thermal stress. As shown on figure 3, all effects of these seven critical biological activities and processes on pup survival and/or growth are rated as poorly understood (low understanding), reflecting a broad lack of published information on the details of the entire life stage. This lack of available information is also reflected in the ratings of "unknown" for link magnitude for almost all effects of the seven critical biological activities and processes on either pup life-stage outcome or the effects of these life-stage outcomes on each other. The CEM, in fact, proposes link magnitudes for the effects of only three critical biological activities or processes on pup survival or growth. Specifically, the CEM hypothesizes that feeding success has a high-magnitude direct effect on both pup growth and pup survival; that disease has a low-magnitude effect on pup survival; and that chemical stress has a low-magnitude effect on both pup survival and pup growth. The estimates of low magnitude for the latter two rest on published estimates of post-natal, pre-weaning survival rates of 95 to 96 percent among Townsend's big-eared bat pups. Such a high rate of survival would indicate a low incidence of illness or mortality from all causes despite the known occurrence of exposure to infectious agents and chemical contaminants.

The CEM proposes that several critical biological activities and processes for this life stage affect each other, possibly compounding their effects on pup growth or survival. Specifically, the CEM proposes that chemical stress, disease, mechanical stress, and thermal stress all affect feeding; that disease and thermal stress affect each other; and that predation affects mechanical stress; however, the CEM identifies the magnitudes of all these links among critical biological activities and processes as unknown, with proposed low understanding, due to the lack of published information on these topics for this or any closely related species. The CEM proposes these links based on suggestions in the published literature on Townsend's big-eared bats and on basic principles of bat biology.

The CEM identifies two habitat elements with direct, high-magnitude effects on one or more of the seven critical biological activities or processes that shape this life stage. Most importantly, maternal care directly affects pup growth and survival in four ways: (1) through the provision of food to the pups (one pup per mother), (2) through maternal selection of the maternity roosting location, (3) through various behaviors that protect the pups from thermal stress and ectoparasites, and (4) through behaviors to protect pups from predators. The CEM rates the first of these three causal relationships as well understood; the second and third as moderately understood; and the fourth as poorly understood.

The CEM proposes the last of these four links based on suggestions in the published literature on Townsend's big-eared bats and on basic principles of bat biology.

The CEM also identifies the vertebrate community as a habitat element with a high-magnitude effect on a critical biological activities or process; in this case, predation. The composition, abundance, and activity level of the vertebrate community around the openings to maternity roosts establish the spectrum of vertebrates that could enter and attempt to prey on Townsend's big-eared bats, including pups, in the maternity roosts. However, the literature reviewed for this CEM does not provide information on what species may prey on the pups. The CEM proposes this relationship based on suggestions in the published literature on Townsend's big-eared bats and on basic principles of bat biology.

The CEM identifies only two other habitat elements that can affect any of the seven critical biological activities or processes that shape this life stage for which the literature provides sufficient information to support an estimate of link magnitude. First, the CEM proposes that anthropogenic disturbance can directly disrupt pup feeding; however, it proposes that this link has low magnitude and low understanding: anthropogenic disturbance affects many critical biological activities and processes for Townsend's big-eared bat pups, with proposed high magnitude, by disrupting maternal care (see below, this chapter, "Life Stage 2 – Adults"). Second, the CEM proposes that the air temperature in maternity roost sites affects the incidence of thermal stress in Townsend's big-eared bat pups. The CEM proposes that this link has low magnitude and moderate understanding because the literature indicates that maternal care strongly mediates pup vulnerability to any such thermal stress.

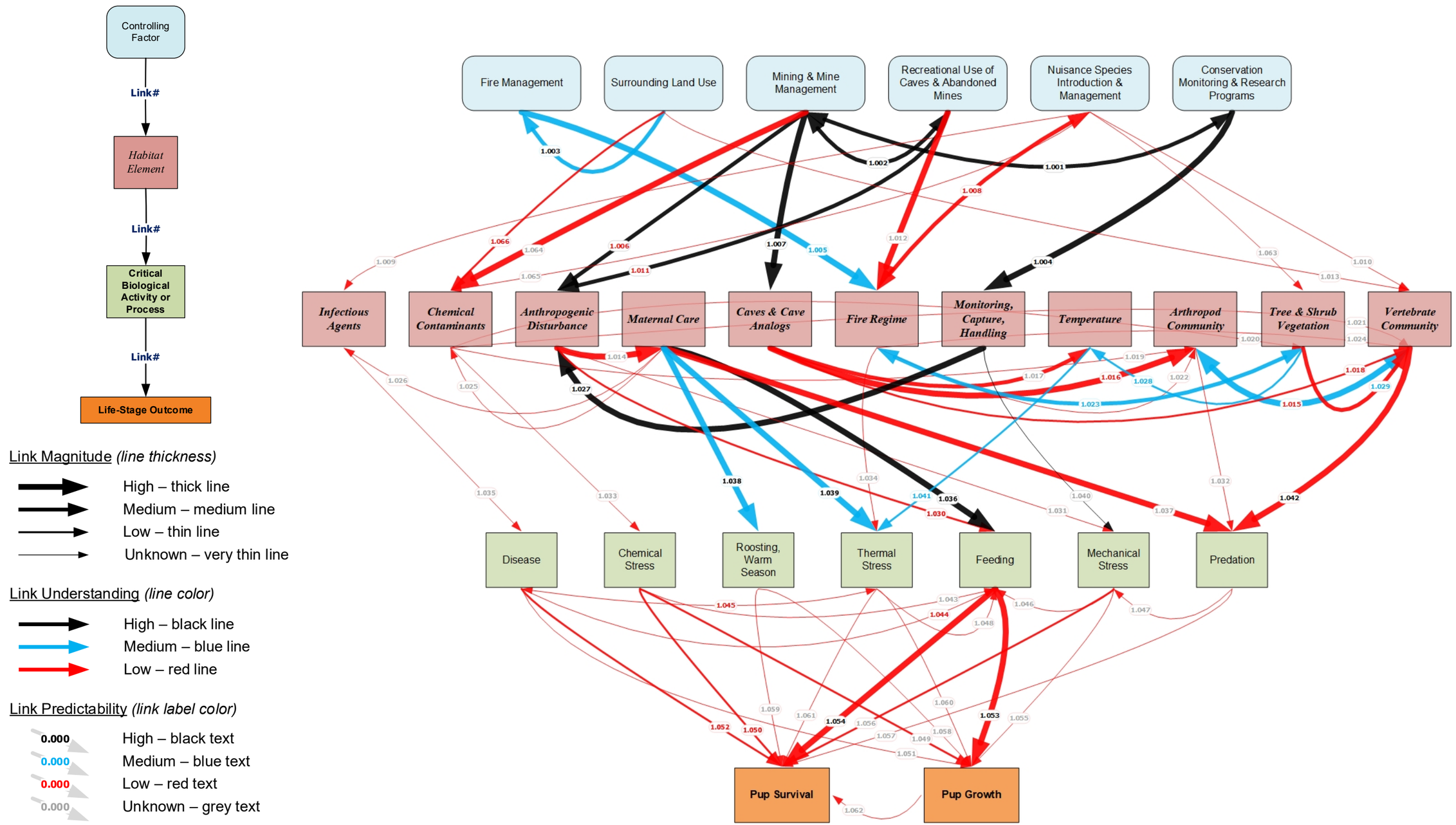

Figure 3.—CEM master diagram for Townsend's big-eared bat life stage 1 – pup life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LIFE STAGE 2 – JUVENILES

As described in chapter 2, the Townsend's big-eared bat juvenile life stage begins when pups are weaned but ends at different times for different parts of the juvenile population. Females may become sexually mature and mate shortly before or after they join a hibernaculum, as soon as 3 months after weaning, while all other females and all males become reproductively active after they complete their first year of life. The juvenile life stage, thus, may span as little as 3 months or as many as 11 months, ending either with the onset of their first season of reproductive activity or the end of their first year of life, whichever comes first. After their first winter, juvenile males and juvenile non-reproductive females join so-called bachelor colonies, while reproductive female yearlings (now adults) join maternity colonies. Bachelor and maternity colonies may be located in different parts of the same cave or cave analog.

This life stage has two life-stage outcomes (see figure 1): juvenile growth and juvenile survival. Since Townsend's big-eared bat pups grow to nearly their full adult size by the time they are volant, little increase in body mass occurs during the juvenile life stage. Growth instead consists mostly of physiological—particularly sexual—maturation and the maintenance of body mass, seasonal fat reserves, and strength. Juvenile survival is estimated to be only 38 to 54 percent. Figure 4 (at the end of this section) presents the complete CEM for this life stage, showing all controlling factors, habitat elements, critical biological activities and processes, life-stage outcomes, and their linkages.

The CEM proposes that juvenile growth affects juvenile survival but with unknown magnitude. As noted above (also see attachment 1), link magnitude refers to the degree to which a given component of the model controls some condition relative to other components affecting that same condition. Theoretically, faster maturation in Townsend's big-eared bat juveniles should convey lower vulnerability to threats specific to the juvenile life stage and, therefore, lead to a higher rate of survival. The relationship should be strong, based on core biological principles; however, no studies have addressed the topic specifically for Townsend's big-eared bats or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is low.

The CEM identifies six critical biological activities or processes that directly affect juvenile survival; however, only two of these, foraging and predation, are proposed to have high-magnitude effects on this life-stage outcome. All other direct effects of critical biological activities or processes on juvenile survival are rated as unknown for magnitude and low for understanding.

Townsend's big-eared bat juveniles that do not forage effectively simply die or suffer higher levels of predation. As noted above, the literature reports juvenile annual survival rates of 38 to 54 percent; however, the literature does not attempt

to break down these figures by potential cause, and it is generally considered difficult to separate causes of mortality among bats (Messenger et al. 2003). On the other hand, Gruver and Keinath (2006) note, "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." For this reason, the CEM hypothesizes that foraging success among Townsend's big-eared bat juveniles is crucial to their surviving their first cold season, while noting that the proposed link has low understanding.

Similarly, vertebrates that could prey on Townsend's big-eared bat juveniles are present throughout the greater LCR ecosystem (see chapter 4, "Vertebrate Community"); however, no information exists on the effect of specific predators on Townsend's big-eared bat juvenile survival in the greater LCR ecosystem or elsewhere. Again, as noted above, the literature does not attempt to break down juvenile survival figures by potential cause, and it is generally considered difficult to separate causes of mortality among bats (Messenger et al. 2003). On the other hand, Gruver and Keinath (2006) also state:

> *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.*

As noted in chapter 3 (see "Predation"), Mikula et al. (2016) suggest that diurnal avian (particularly raptor) predation is a major source of mortality for bats worldwide. This CEM hypothesizes that this is the case for Townsend's big-eared bat juveniles, which at least initially in this life stage are necessarily less experienced at evading predators. At the same time, the CEM recognizes that the subject remains unstudied in the Lower Colorado River Valley or elsewhere, necessitating a link rating of low for understanding.

The CEM identifies five critical biological activities or processes that directly affect juvenile growth; however, only one of these, foraging, is proposed to have high-magnitude effects on this life-stage outcome. All other direct effects of critical biological activities or processes on juvenile growth are rated as unknown for magnitude and low for understanding.

The CEM proposes a strong effect of foraging success on Townsend's big-eared bat juvenile growth simply because obtaining food is essential for juvenile growth in any species. As noted above, the building of fat reserves is an important process for Townsend's big-eared bat juveniles leading up to their first winter; however, the incidence of sufficient versus insufficient feeding among Townsend's big-eared bat juveniles is unknown in the Lower Colorado River Valley or elsewhere. The CEM therefore rates the link as low for understanding.

The CEM proposes that several of the critical biological activities and processes for the juvenile life stage affect each other, possibly compounding their effects on juvenile growth or survival. Most of these links are proposed based on suggestions in the published literature on Townsend's big-eared bats and on basic principles of bat biology and are rated as unknown for magnitude and low for understanding. However, the CEM suggests stronger ratings for link magnitude for four links among critical biological activities and processes.

Specifically, the CEM proposes that roosting site requirements and search behaviors for both cold- and warm-season roosting sites are important drivers of inter-site movement, with proposed medium magnitude but low understanding. The literature clearly indicates that disruption to a hibernaculum can trigger inter-site movement, but it does not document the likely frequency of such events following abandonment of cold-season roosting sites more generally, and the occurrence of such events is necessarily highly situation specific. Similarly, the literature reports individual instances of warm-season roosting site abandonment and inter-site movement following disturbance. For example, Townsend's big-eared bats abandoned Mountaineer Mine in the Riverside Mountains, California, above the LCR in August 2016, following disturbance by a monitoring team (Maturango Museum and Brown-Berry Biological Consulting 2018; Brown, *in press*). Again, the literature does not document the likely frequency of such events in general, and the occurrence of such events is necessarily highly situation specific. Further, the literature on such events does not distinguish adult from juvenile inter-site movement.

The CEM also proposes that both competition and predation might disrupt foraging by Townsend's big-eared bat juveniles, but it also proposes rating the links as low for both magnitude and understanding. There is no evidence that Townsend's big-eared bats compete with other bat species for food or roosting habitat. Insectivorous bats have evolved in close competition with each other for millions of years, resulting in extensive resource partitioning. Such partitioning includes targeting different types of prey, in different environmental settings, at different times of night (Gruver and Keinath 2006). Nevertheless, competition, at least for prey, is a theoretical possibility, although unstudied specifically for Townsend's big-eared bats. Similarly, theoretically, foraging Townsend's big-eared bats can detect prowling predators and seek shelter or alter their foraging behaviors to reduce the chances of becoming a meal for another species. However, the literature reports great consistency in Townsend's big-eared bat foraging movement patterns, suggesting that the species may not be disrupted by predator activity in their midst. On the other hand, the literature does not report any systematic studies of the topic along the Lower Colorado River Valley or elsewhere.

The CEM identifies 11 habitat elements that may affect 1 or more critical biological activities or processes in the juvenile life stage. Each of these 11 habitat elements is proposed to directly affect at least 1 critical biological

activity or process; however, only 6 habitat elements are proposed to have high-magnitude effects on any critical biological activity or process. The CEM proposes that anthropogenic disturbance can significantly disrupt both warm- and cold-season roosting; cave and cave analog characteristics similarly have high-magnitude effects on site selection and success for both warm- and cold-season roosting; interior temperatures in caves and cave analogs also have high-magnitude effects on roosting site selection and success for both warm- and cold-season roosting; the arthropod community and tree and shrub vegetation across existing and potential foraging habitat affect Townsend's big-eared bat foraging behaviors and success with proposed high magnitude; and the vertebrate community across the landscapes where Townsend's big-eared bats forage and roost affect the rate of predation on the bats with high magnitude.

The effects of cave and cave analog characteristics on both warm- and cold-season roosting site selection and success are rated as high for understanding. Both topics are well reported; however, all other high-magnitude direct effects of habitat elements on critical biological activities or processes for the juvenile life stage are rated as low for understanding.

The CEM proposes that two habitat elements each have a medium-magnitude effect on a critical biological activity or process for the juvenile life stage. Cave and cave analog characteristics are proposed to affect interim roosting behaviors and site selection with proposed medium understanding. The arthropod community is proposed to affect roosting site selection during the warm season, also with proposed medium understanding. Townsend's big-eared bat juveniles (and adults) are proposed to ignore or move away from potential warm-season roosting sites when the arthropod community within foraging distance of a site does not meet the food requirements of the bats.

The CEM identifies three other habitat elements that potentially can affect one or more critical biological activities or processes for this life stage with proposed low magnitude. First, the CEM proposes that anthropogenic disturbance can have low-magnitude effects on interim roosting and foraging, but it rates these links as having low understanding. Second, the CEM proposes that tree and shrub vegetation around the openings of caves and cave analogs can have low-magnitude effects on both cold- and warm-season roosting site selection, but it again rates these links as having low understanding. Third, the CEM proposes that water availability can have low-magnitude effects on both cold- and warm-season roosting site selection and on chemical stress, rating all three of these latter links as having moderate understanding.

Finally, one habitat element reciprocally is affected with proposed high magnitude by one of the critical biological activities or processes in the juvenile life stage. Townsend's big-eared bat juvenile (and adult) foraging behaviors affect the ease with which they can be detected by acoustic monitoring equipment or captured in mist nets in different settings. Townsend's big-eared bat

echolocation calls are notoriously faint, resulting in their being called a whispering bat. Their low-decibel calls can only be detected and accurately distinguished when they fly within a limited distance of an acoustic monitoring station. The propensity of the species to forage along the edges of tree and shrub patches and the edges of different canopy tiers within these patches also affect where and how readily they can be detected or captured. Investigators seeking to monitor Townsend's big-eared bat juvenile (and adult) foraging behaviors consequently need to take these interactions into account in order to acquire representative samples of call records or to capture representative samples of foraging bats.

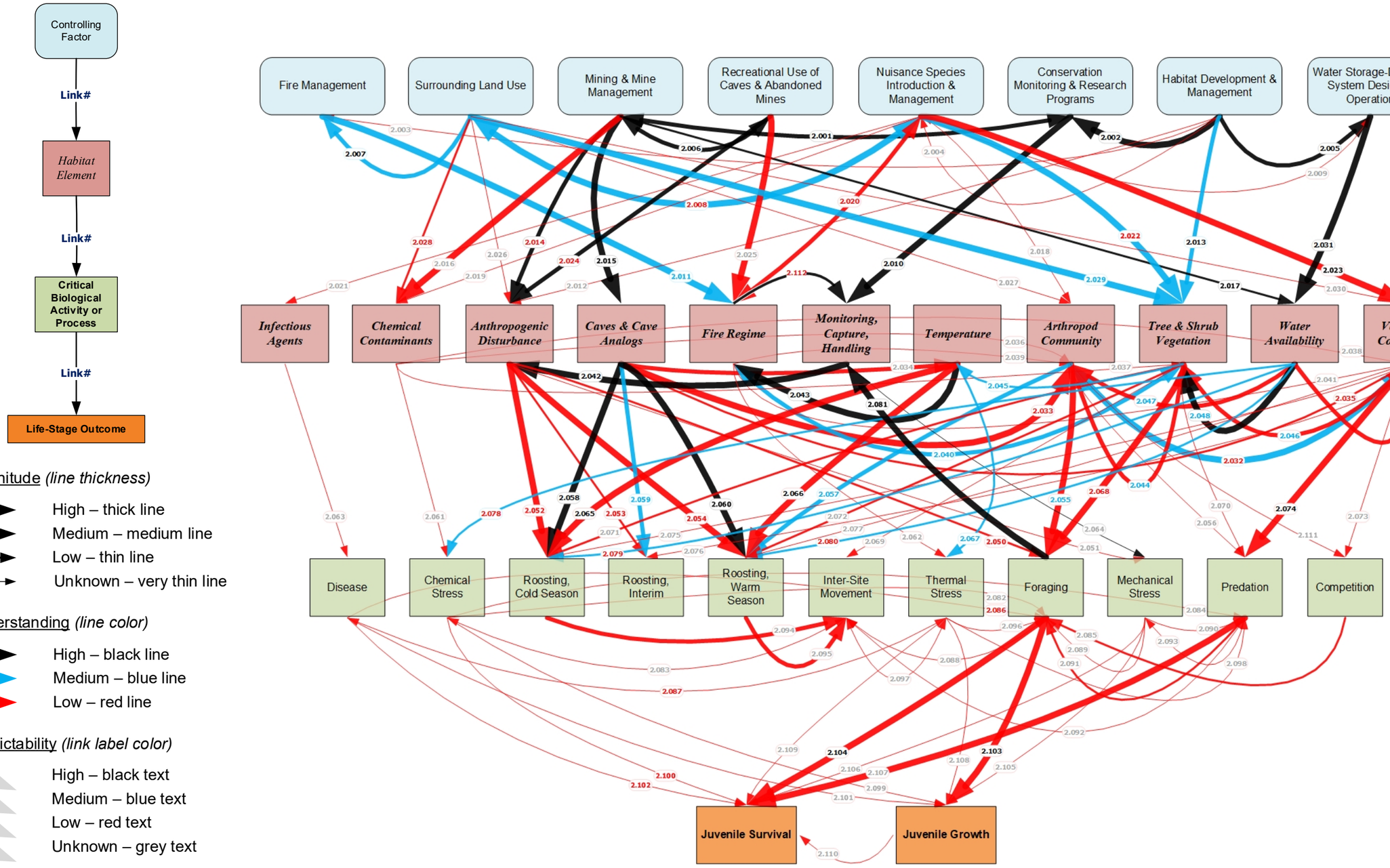

Figure 4.—CEM master diagram for Townsend's big-eared bat life stage 2 – juvenile life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LIFE STAGE 3 – ADULTS

As described in chapter 2, the Townsend's big-eared bat adult life stage begins when juveniles become sexually mature, which can occur at different times for different parts of the juvenile population. Females may become sexually mature and mate as soon as 3 months after weaning, during autumn of their first year of life, shortly before or after they join a hibernaculum. All other females and all males become reproductively active after they complete their first year of life, mating for the first time during autumn of their second year. As noted in chapter 1, the literature reports a typical maximum lifespan for Townsend's big-eared bats of approximately 16 years in the wild, with an average lifespan and a possible generation time (average difference in age between parent and offspring) of approximately 5 years.

The CEM for the adult life stage resembles that for the juvenile life stage in many respects but differs in two large, important ways. First, the adult life stage includes critical biological activities and processes and a life-stage outcome related to reproduction. Second, the literature on the Townsend's big-eared bat provides far more information on the adult life stage than on the juvenile life stage; in fact, much of the CEM for the juvenile stage rests on knowledge of the adult life stage, with the presumption that, except for dynamics related to reproduction, juvenile Townsend's big-eared bats mostly behave very similarly to adults.

The CEM for the Townsend's big-eared bat adult life stage has three life-stage outcomes (see figure 1): adult growth, adult survival, and adult fertility. Adults do not appear to grow larger as they age; growth, instead involves the maintenance of seasonal fat reserves and strength and seasonal physiological changes to support reproduction and maternal care. Adult annual survival is estimated to be at least 70 to 80 percent, but this range likely underestimates actual survival. The estimate comes from recapture data for banded adults returning to their natal warm-season roosting site, which are shaped by both mortality and inter-site dispersal. Figure 5 (at the end of this section) presents the complete CEM for this life stage, showing all controlling factors, habitat elements, critical biological activities and processes, life-stage outcomes, and their linkages.

Similar to the CEMs for the pup and juvenile life stages, the CEM for the adult life stage proposes that adult growth affects adult survival but with unknown magnitude. As noted above (also see attachment 1), link magnitude refers to the degree to which a given component of the model controls some condition relative to other components affecting that same condition. Theoretically, better growth in Townsend's big-eared bat adults (i.e., better maintenance of body mass and strength) should convey lower vulnerability to threats specific to the adult life stage and, therefore, lead to a higher rate of survival. The relationship should be

strong, based on core biological principles; however, no studies have addressed the topic specifically for Townsend's big-eared bats or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is low.

The CEM for the adult life stage also proposes that adult growth and adult survival both affect fertility, but with unknown magnitude. Theoretically, growth—i.e., maintenance of body mass and seasonal readiness for reproduction—is crucial to Townsend's big-eared bat fertility. Logically, only adults that survive from one reproductive season to the next can continue to reproduce. These relationships should be strong, based on core biological principles; however, no studies have addressed the topic specifically for Townsend's big-eared bats or any closely related species. As a result, the magnitudes of these two links are unknown, and link understanding is low for both.

The CEM identifies six critical biological activities or processes that directly affect adult survival; however, only three of these—chemical stress, foraging, and predation—are proposed to have high-magnitude effects on this life-stage outcome. All other direct effects of critical biological activities or processes on adult survival are rated as unknown for magnitude and low for understanding.

Chemical stress can be fatal in any life stage of any animal species. The higher the level of chemical stress experienced by an adult bat, the lower their likely rate of survival. The literature on the Townsend's big-eared bats specifically mentions the possibility of mortality or impaired health from exposure to soluble metals and mining industrial wastes due to roosting in abandoned underground mines, including drinking from contaminated waters within or associated with such underground mines. Some metals may bioaccumulate in Townsend's big-eared bat body tissues; however, no literature exists on Townsend's big-eared bat exposure risk to chemicals in LCR open environments, although the impacts have been identified as a topic of concern. As noted above, the literature does not attempt to break down Townsend's big-eared bat mortality data by potential cause, and it is generally considered difficult to separate causes of mortality among bats (Messenger et al. 2003). Consequently, the CEM for the adult life stage rates understanding as low for the possible effects of chemical stress on survival.

Townsend's big-eared bat adults that do not forage effectively simply die from starvation, die from complications of other sources of stress, or suffer higher levels of predation. As noted above, the literature reports adult annual minimum survival rates of 70 to 80 percent. However, again, the literature does not attempt to break down these figures by potential cause, and it is generally considered difficult to separate causes of mortality among bats (Messenger et al. 2003). The CEM therefore identifies this proposed link as having a low level of understanding.

Similarly, vertebrates that could prey on Townsend's big-eared bat adults are present throughout the greater LCR ecosystem (see chapter 4, "Vertebrate Community"). However, no information other than anecdotes exists on the effect of specific predators on Townsend's big-eared bat adult survival in the greater LCR ecosystem or elsewhere. Again, as noted above, the literature does not attempt to break down adult survival figures by potential cause, and it is generally considered difficult to separate causes of mortality among bats (Messenger et al. 2003). On the other hand, Mikula et al. (2016) suggest that diurnal avian (particularly raptor) predation is a major source of mortality for bats worldwide. This CEM hypothesizes that this is the case for Townsend's big-eared bat adults. At the same time, the CEM recognizes that the subject remains unstudied in the Lower Colorado River Valley or elsewhere, necessitating a link rating of low for understanding.

The CEM identifies five critical biological activities or processes that directly affect adult growth. However, only two of these, chemical stress and foraging, are proposed to have high-magnitude effects on this life-stage outcome. All other direct effects of critical biological activities or processes on adult growth are rated as unknown for magnitude and low for understanding.

Chemical stress can impair growth in any life stage of any animal species as discussed in chapter 3. The higher the level of chemical stress experienced by an adult bat, the lower their likely rate of growth. The literature on Townsend's big-eared bats specifically mentions the possibility of impaired health from three sources:

- Exposure to soluble metals and mining industrial wastes due to roosting in abandoned underground mines, including drinking from contaminated waters within or associated with such underground mines. Some metals may bioaccumulate in body tissues.

- Ingestion of insects exposed to pesticides, including organochlorine compounds, and subsequent bioaccumulation of the pesticides and/or their breakdown products. The European Food Safety Authority (Hernández-Jerez et al. 2019) recognizes pesticide exposure as a significant threat to insectivorous bats worldwide.

- Exposure to high rates of radon absorption when roosting in caves and abandoned uranium mines, "… but the health effects of such exposure remain unknown" (O'Shea et al. 2018).

This CEM hypothesizes that these potentially serious risks exist for Townsend's big-eared bat adults. At the same time, the CEM recognizes that the subject remains unstudied in the Lower Colorado River Valley or elsewhere, necessitating a link rating of low for understanding.

Chemical stress potentially also can impair Townsend's big-eared bat fertility. The CEM recognizes this relationship by including a high-magnitude effect of chemical stress on another critical biological activity or process, breeding, as discussed below.

The CEM proposes a strong effect of foraging success on Townsend's big-eared bat adult growth simply because obtaining food is essential for growth in any species. As noted above, growth for Townsend's big-eared bat adults involves the maintenance of seasonal fat reserves and strength and seasonal physiological changes to support reproduction and maternal care; however, the incidence of sufficient versus insufficient feeding among Townsend's big-eared bat adults is unknown in the Lower Colorado River Valley or elsewhere. The CEM therefore rates the link as low for understanding.

The CEM for the adult life stage identifies two critical biological activities or processes that directly affect fertility, breeding and maternal care, both with proposed high magnitude. The rate of participation of Townsend's big-eared bat adults in breeding and their breeding success (fecundity, which is affected by maternal care, as discussed below), together with adult survival, determine Townsend's big-eared bat fertility. Anecdotally, disruptions to Townsend's big-eared bat breeding can cause reproductive females to abort their single embryo; however, there are no systematic data available on the subject for Townsend's big-eared bats in the Lower Colorado River Valley or anywhere else. Consequently, the CEM rates understanding as low for this relationship.

Maternal care likely also has a large effect on Townsend's big-eared bat reproductive success. In the extreme, in fact, disruptions to maternity colonies can cause both individual and entire colonies of lactating females to abandon their pups (and abandon the entire site) before weaning, resulting in complete reproductive failure of that colony for the year; however, again, there are no systematic data available on the subject for Townsend's big-eared bats in the Lower Colorado River Valley or anywhere else. Consequently, the CEM rates understanding as low for this relationship.

The CEM proposes that several of the critical biological activities and processes for the adult life stage affect each other, possibly compounding their effects on adult growth, survival, and fertility. Most of the resulting 27 links between individual critical biological activities and processes are proposed based on suggestions in the literature on Townsend's big-eared bats and on basic principles of bat biology and rated as unknown for magnitude and low for understanding. However, the CEM suggests stronger magnitude (high, medium, or low) ratings for seven links among critical biological activities and processes, as follows:

- The CEM for the adult life stage proposes that foraging success for pregnant and nursing females affects their success in breeding and in providing maternal care, with proposed high magnitude. Foraging success affects the ability of the mother to successfully gestate and give birth to a healthy pup. Anecdotally, food-stressed pregnant Townsend's big-eared bats may abort their embryos. Similarly, foraging success affects the ability of the mother to provision for her young and attend the roost, including protecting the pup from thermal stress. Anecdotally, food-stressed lactating Townsend's big-eared bats may even abandon their pups. The two links are rated as low for understanding due to a lack of systematic coverage in the literature on the species in the greater Lower Colorado River Valley or elsewhere.

- The CEM for the adult life stage proposes that breeding success also depends, with proposed high magnitude, on successful selection of a suitable roosting site by reproductive females for both the warm and cold seasons (i.e., for their maternal roosting site and their hibernaculum). Successful selection can include moving to a new site when needed (e.g., to avoid disturbance or adjust roosting location to take advantage of changes in temperature distributions within a cave or underground mine). The two links are rated as low for understanding due to a lack of systematic coverage in the literature on the species in the greater Lower Colorado River Valley or elsewhere.

- The CEM for the adult life stage proposes that inter-site movements among Townsend's big-eared bats are partly driven by reproductive female efforts to find suitable roosting sites for both the warm and cold seasons (i.e., for their maternal roosting site and their hibernaculum). The CEM proposes that these two links have medium magnitude. The Townsend's big-eared bat annual cycle of inter-site movement is likely driven by climate, weather, and photoperiod, and the species shows strong fidelity to their natal warm-season roosting area and year-one hibernaculum as well as strong fidelity to particular foraging areas and the routes they follow to those foraging areas from their warm-season roosts. However, Townsend's big-eared bats are known to abandon a warm-season roosting site or a hibernaculum when disturbed or when changes in an inactive underground mine (e.g., reactivation or sealing of entrances) that the species has previously occupied make it unavailable. The bats then seek and move to another warm- or cold-season roosting site. However, while the literature indicates anecdotally that disruption to a hibernaculum can trigger inter-site movement, it does not document the likely frequency of such events, which are likely highly situation specific. Similarly, the literature reports specific instances of Townsend's big-eared bat abandonment of warm-season roosting sites following disturbance (e.g., when they abandoned Mountaineer Mine in the Riverside Mountains, California, above the LCR in August 2016, following

disturbance by a monitoring team). However, the literature does not document the likely frequency of such events in general, and the occurrence of such events is again likely highly situation specific. For these reasons, the CEM rates understanding as low for both of these proposed links.

- Finally, the CEM proposes that both competition and predation might disrupt foraging by Townsend's big-eared bat adults but also proposes rating the links as low for both magnitude and understanding. As discussed above, the literature does not report evidence that Townsend's big-eared bats compete with other bat species for food or roosting habitat. Insectivorous bats have evolved in close competition with each other for millions of years, resulting in extensive resource partitioning. Such partitioning includes targeting different types of prey, in different environmental settings, at different times of night (Gruver and Keinath 2006). Nevertheless, competition, at least for prey, is a theoretical possibility, although unstudied specifically for Townsend's big-eared bat. It is similarly conceivable that, while foraging, Townsend's big-eared bats can detect prowling predators and seek shelter or alter their foraging behaviors to reduce the chances of becoming a meal for another species. However, the literature reports great consistency in Townsend's big-eared bat foraging movement patterns, suggesting that the species may not be disrupted by predator activity in their midst. On the other hand, the literature does not report any systematic studies of the topic in general or along the Lower Colorado River Valley in particular.

The CEM identifies 11 habitat elements that may affect 1 or more critical biological activities or processes in the adult life stage. Each of these 11 habitat elements is proposed to directly affect at least 1 critical biological activity or process; however, only 6 habitat elements are proposed to have high-magnitude effects on any critical biological activity or process. Specifically, the CEM for the adult life stage proposes the following:

- Anthropogenic disturbance can strongly affect (significantly disrupt) breeding, maternal care, and both warm- and cold-season roosting. The CEM proposes that the effects of anthropogenic disturbance on breeding are moderately well understood from numerous anecdotal observations (see above, effects of breeding and maternal care on fertility). At the same time, the CEM proposes that the effects of anthropogenic disturbance on maternal care and both warm- and cold-season roosting are less well documented and, therefore, warrant ratings of low for understanding.

- The arthropod community and tree and shrub vegetation across existing and potential foraging habitat affect Townsend's big-eared bat adult foraging behaviors and success; however, the CEM proposes that these effects are not well documented and, therefore, warrant ratings of low for understanding.

- Cave and cave analog characteristics strongly affect site selection and roosting success for both warm- and cold-season roosting. The CEM proposes that both of these effects are well documented and well understood in the literature.

- Interior temperatures in caves and cave analogs also strongly affect roosting site selection and roosting success for both warm- and cold-season roosting; however, the CEM proposes that these effects are not well documented and, therefore, warrant ratings of low for understanding.

- The composition and spatial structure of the tree and shrub vegetation strongly directly affect foraging behaviors and success, with proposed high magnitude; however, the CEM proposes that these effects are not well documented and, therefore, warrant ratings of low for understanding.

- The vertebrate community across the landscapes where Townsend's big-eared bat adults forage and roost strongly affect the rate of predation on the bats. Again, however, the CEM proposes that these effects are not well documented and, therefore, warrant ratings of low for understanding.

The CEM also identifies six habitat elements that may affect one or more critical biological activities or processes in the adult life stage, with proposed medium or low magnitude. Specifically, the CEM for the adult life stage proposes the following:

- Anthropogenic disturbance may disrupt Townsend's big-eared bat adult foraging and interim roosting, with proposed low magnitude. The links are proposed to have low understanding.

- The arthropod community is proposed to affect roosting site selection during the warm season. Townsend's big-eared bat adults are proposed to ignore or move away from potential warm-season roosting sites when the arthropod community within foraging distance of a site does not meet their food requirements. The link is proposed to have medium understanding.

- Cave and cave analog characteristics are proposed to affect interim roosting behaviors and site selection, with proposed medium understanding.

- Interior temperatures in caves and cave analogs are proposed to have a low-magnitude effect on thermal stress in roosting adults. Townsend's big-eared bat adults have been observed to cluster together for mutual thermal regulation while roosting and to move to alternative locations within caves or underground mines or to alternative caves or underground mines to find roosting locations that do not cause them thermal stress. The link is proposed to have medium understanding.

- Tree and shrub vegetation around the openings of caves and cave analogs are proposed to have low-magnitude effects on both cold- and warm-season roosting site selection. Again, however, these links are rated as having low understanding.

- The CEM proposes that water availability can have low-magnitude effects on both cold- and warm-season roosting site selection and on chemical stress. The CEM rates all three of these links as having moderate understanding.

Finally, the CEM proposes that one critical biological activity or process in the adult life stage reciprocally has high-magnitude effects on one habitat element. Townsend's big-eared bat adult foraging behaviors affect the ease with which they can be detected by acoustic monitoring equipment or captured in mist nets in different settings. As discussed above, Townsend's big-eared bat echolocation calls are notoriously faint, resulting in their being called a whispering bat. Their low-decibel calls can only be detected and accurately distinguished when they fly within a limited distance of an acoustic monitoring station. The tendency of the species to forage along the edges of tree and shrub patches and the edges of different canopy tiers within these patches also affect where and how readily they can be detected or captured. Investigators seeking to monitor Townsend's big-eared bat adult foraging behaviors consequently need to take these interactions into account in order to acquire representative samples of call records or to capture representative samples of foraging bats.

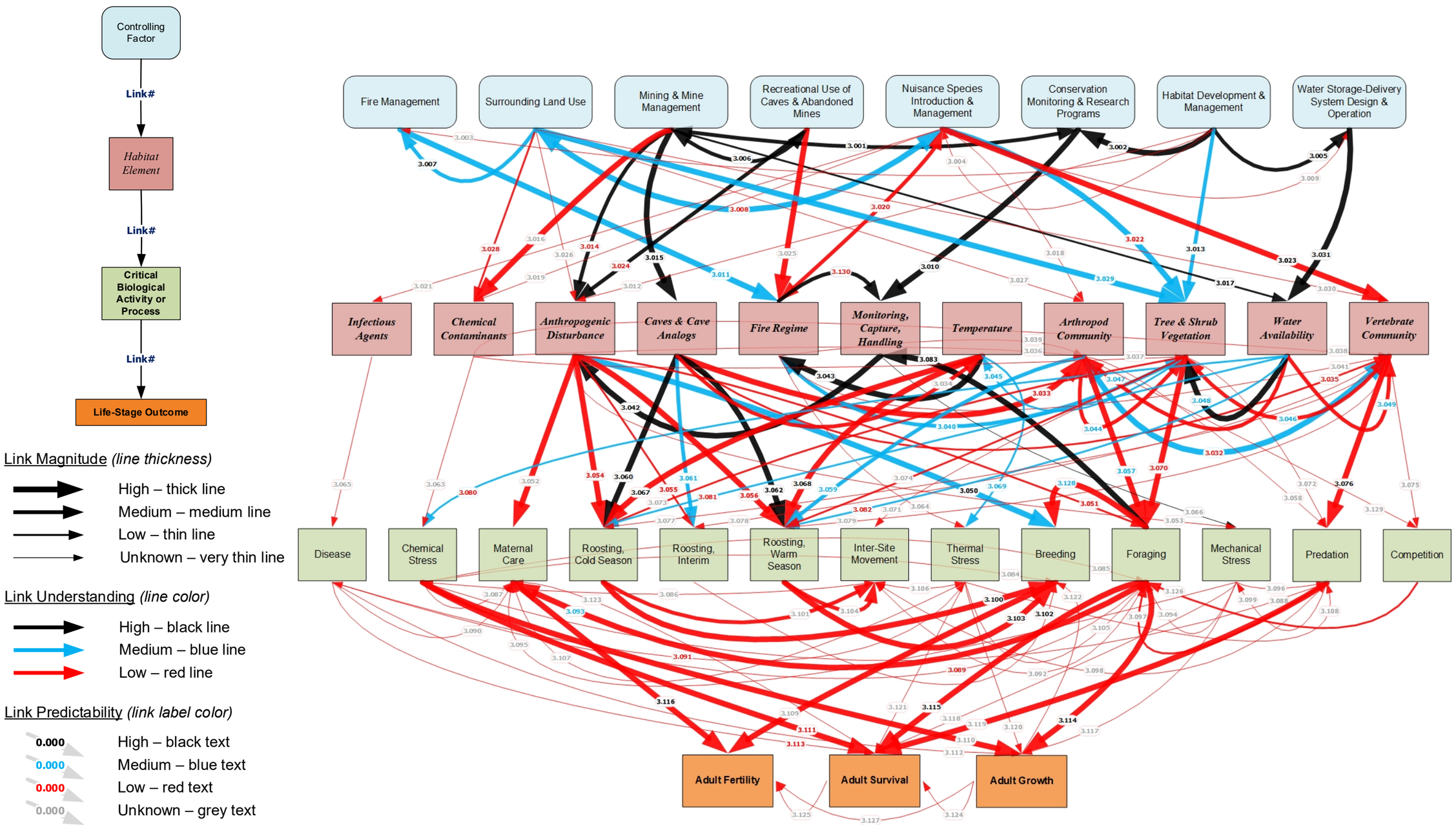

Figure 5.—CEM master diagram for Townsend's big-eared bat life stage 3 – adult life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

Chapter 7 – Causal Relationships Across All Life Stages

Chapter 6 focuses on four types of causal relationships in the CEMs for each of the three Townsend's big-eared bat life stages: causal relationships (1) among life-stage outcomes, (2) between critical biological activities and processes and life-stage outcomes, (3) among critical biological activities and processes, and (4) between habitat elements and critical biological activities and processes. These four sets of relationships differ in many respects between life stages. This chapter focuses on three additional types of causal relationships across the three life stages: causal relationships (5) among habitat elements, (6) between controlling factors and habitat elements, and (7) among controlling factors. The latter three sets of relationships are essentially the same across all three life stages.

This chapter discusses these last three types of causal relationships in two groups—relationships that affect Townsend's big-eared bat activities mostly within the LCR MSCP planning area and relationships that affect the activities of the species mostly in the uplands surrounding the planning area. This is not an arbitrary distinction: As discussed in chapter 1, the caves and underground mines that Townsend's big-eared bats use as cold- and warm-season roosting sites in the greater LCR ecosystem occur only in upland settings with exposed bedrock. This distribution reflects the geology and history of underground mining in the region. As also noted in chapter 1, the upland areas with cold- and warm-season roosting sites all lie outside the LCR MSCP planning area. Conversely, Townsend's big-eared bats commute from their warm-season roosting sites in these uplands to reach foraging habitat mostly within and immediately around the historic LCR floodplain, where they forage and seek out night roosting sites for feeding on larger prey. This zone of commuting, foraging, and night roosting loosely encompasses the LCR MSCP planning area.

Nearly two decades of investigations in the greater Lower Colorado River Valley document this broad geographic separation of activities (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Brown 2010, 2013; Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Diamond 2012; Diamond et al. 2013; Hill 2018; LCR MSCP 2008, 2009; Maturango Museum and Brown-Berry Biological Consulting 2018; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2012, 2013; Brown, *in press*; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010). The distinction potentially is important to the management of habitat for Townsend's big-eared bats. LCR MSCP management responsibilities under the HCP lie only within its authorized planning area, while Federal, State, and Tribal partner agencies oversee species and habitat management in the surrounding uplands.

CAUSAL RELATIONSHIPS AFFECTING COLD- AND WARM-SEASON ROOSTING HABITAT

The text and figures in chapter 6 identify the habitat elements that may affect cold- and warm-season roosting by Townsend's big-eared bats across the uplands surrounding the historic LCR floodplain with proposed high, medium, low, or unknown magnitude. These habitat elements include the following:

- Anthropogenic disturbance, caves and cave analogs, and temperature, with proposed high-magnitude effects on both cold- and warm-season roosting.
- The arthropod community, with proposed medium-magnitude effects on warm-season roosting.
- The tree and shrub vegetation and water availability, with proposed low-magnitude effects on both cold- and warm-season roosting.
- The vertebrate community, with unknown-magnitude effects on both cold- and warm-season roosting.

In turn, these seven habitat elements are directly affected by other habitat elements. Specifically, the CEM proposes the following:

- Anthropogenic disturbance is affected by monitoring, capture, handling, and tree and shrub vegetation is affected by water availability, both with proposed high magnitude and high understanding.
- In and immediately around caves and cave analogs, the vertebrate community is affected by the arthropod community, with proposed high magnitude and medium understanding.
- The arthropod community in caves and cave analogs is affected by cave and cave analog characteristics, with proposed high magnitude but low understanding.
- The tree and shrub vegetation around the openings to caves and cave analogs is affected by the fire regime in this setting, with proposed medium magnitude and medium understanding.
- Air temperature variation within caves and cave analogs is affected by cave and cave analog characteristics, and the arthropod and vertebrate communities in and immediately around caves and cave analogs are both affected by the tree and shrub vegetation and water availability in these settings, all with proposed medium magnitude and low understanding.

- Air temperature variation within caves and cave analogs is affected by the tree and shrub vegetation around the openings to these geological features, with proposed low magnitude and medium understanding.

- The vertebrate community in caves and cave analogs is affected by cave and cave analog characteristics, with proposed low magnitude and low understanding.

- The arthropod and vertebrate communities in and immediately around cave and cave analogs, and the tree and shrub vegetation around cave and cave analog openings, are all affected by chemical contaminants in these settings, with unknown magnitude and low understanding.

- The arthropod and vertebrate communities in and immediately around cave and cave analogs also are affected by the fire regime in these settings, including fires that may occur within caves and cave analogs, with unknown magnitude and low understanding.

The CEM thus identifies 10 habitat elements that directly or strongly indirectly affect cold- and warm-season roosting as follows: anthropogenic disturbance; the arthropod community in and immediately around caves and cave analogs; cave and cave analog characteristics; chemical contaminants and the fire regime in and immediately around caves and cave analogs; monitoring, capture, handling of the bats in and immediately around their roosting sites; air temperature within the roosting sites; tree and shrub vegetation immediately around the openings to caves and cave analogs; the vertebrate community; and water availability in and immediately around caves and cave analogs.

The CEM further proposes that these 10 habitat elements, in turn, are shaped by 6 of the 8 controlling factors included in the CEM. Specifically, the CEM proposes the following:

- Conservation monitoring and research programs shape the monitoring, capture, and handling of Townsend's big-eared bats in and immediately around their cold- and warm-season roosting sites, with proposed high magnitude and high understanding.

- Mining and mine management shapes the presence, distribution, and characteristics of underground mines (cave analogs), also with proposed high magnitude and high understanding.

- Fire management shapes the fire regime in the immediate vicinity of caves and cave analogs, and both nuisance species introduction and management and surrounding land use affect the tree and shrub vegetation in these same settings, with proposed high magnitude and medium understanding.

- Mining and mine management affects the presence and concentrations of chemical contaminants in and immediately around caves and cave analogs, nuisance species introduction and management affects the composition of the vertebrate community in these settings, and recreational use of caves and abandoned underground mines affects the fire regime in these settings, all with proposed high magnitude but low understanding.

- Mining and mine management and recreational use of caves and abandoned underground mines both shape the frequency and severity of anthropogenic disturbance at cold- and warm-season roosting sites, with proposed medium magnitude and high understanding.

- Nuisance species introduction and management affects the fire regime immediately around caves and cave analogs, and vice versa, with proposed medium magnitude and low understanding.

- Mining and mine management affects water availability within and immediately around underground mines (cave analogs), with proposed low magnitude but high understanding.

- Surrounding land use affects the presence and concentrations of chemical contaminants immediately around caves and cave analogs, with proposed low magnitude and low understanding.

- Nuisance species introduction and management affects the arthropod community and the presence and concentrations of chemical contaminants immediately around caves and cave analogs, with unknown magnitude and low understanding. Surrounding land use similarly affects the arthropod and vertebrate communities in the immediate vicinities of caves and cave analogs and the incidence of anthropogenic disturbance in these features, again with unknown magnitude and low understanding.

Finally, the CEM proposes that some of these six controlling factors affect each other in ways that ultimately also affect cold- and warm-season roosting. Specifically, the CEM proposes the following:

- Surrounding land use and nuisance species introduction and management reciprocally affect each other, with proposed high magnitude and medium understanding.

- Conservation monitoring and research programs—specifically requests to mine managers concerning mine access and gating—affect mining and mine management, with proposed medium magnitude and high understanding.

- Recreational use of caves and abandoned underground mines, and mining and mine management, affect each other, with proposed medium magnitude and high understanding. Mine management affects recreational access, and the demands of recreational users affect decisions by managers of active and inactive underground mines concerning such access.

- Surrounding land use affects fire management in the immediate vicinities of caves and cave analogs, with proposed medium magnitude and medium understanding.

CAUSAL RELATIONSHIPS AFFECTING FORAGING, COMMUTING, AND NIGHT-ROOSTING HABITAT

Similarly, the text and figures in chapter 6 identify eight habitat elements that may particularly affect commuting, foraging, night roosting (interim roosting), and other critical biological activities or processes for Townsend's big-eared bats within and immediately around the historic LCR floodplain, with proposed high, medium, low, or unknown magnitude. These eight habitat elements are:

- Anthropogenic disturbance, with proposed low-magnitude effects on foraging and interim (night) roosting, and unknown-magnitude effects on mechanical stress.

- The arthropod community across this landscape, with proposed high-magnitude effects on foraging and unknown-magnitude effects on competition and predation.

- The availability and quality of cave analogs across this landscape, with proposed medium-magnitude effects on interim (night) roosting.

- Chemical contaminants across this landscape, with unknown-magnitude effects on chemical stress.

- Monitoring, capture, handling in this landscape, with unknown-magnitude effects on mechanical stress.

- The tree and shrub vegetation across this landscape, with proposed high-magnitude effects on foraging and unknown-magnitude effects on inter-site movement and predation.

- The vertebrate community across this landscape, with proposed high-magnitude effects on predation and unknown-magnitude effects on competition and interim (night) roosting.

- Water availability across this landscape, with proposed low-magnitude effects on chemical stress.

In turn, these eight habitat elements are directly affected by other habitat elements across this landscape. Specifically, the CEM proposes the following:

- Anthropogenic disturbance is affected by monitoring, capture, and handling, with proposed high magnitude and high understanding. Tree and shrub vegetation similarly is affected by water availability, with proposed high magnitude and high understanding.

- The arthropod and vertebrate communities affect each other, with proposed high magnitude and medium understanding.

- The arthropod community in cave analogs that the bats use for interim (night) roosting is affected by characteristics of these features, with proposed high magnitude but low understanding.

- Monitoring, capture, handling is affected by the fire regime, with proposed medium magnitude and high understanding.

- The tree and shrub vegetation across this landscape is affected by the local fire regime, with proposed medium magnitude and medium understanding.

- The arthropod and vertebrate communities across this landscape are both affected by the tree and shrub vegetation and by water availability, with proposed medium magnitude but low understanding.

- The vertebrate community using cave analogs that the bats also use for interim (night) roosting is affected by characteristics of these features, with proposed low magnitude and low understanding.

- The arthropod community, tree and shrub vegetation, and vertebrate community across this landscape potentially are affected by chemical contaminants, with unknown magnitude and low understanding.

- The arthropod and vertebrate communities across this landscape potentially are also affected by the fire regime, with unknown magnitude and low understanding.

The full list of habitat elements that the CEM proposes to directly or indirectly (at one remove) affect commuting, foraging, night-roosting (interim roosting), and other critical biological activities or processes for Townsend's big-eared bats within and immediately around the historic LCR floodplain therefore consists of the following nine elements: anthropogenic disturbance; the arthropod community; cave and cave analog characteristics for features used for night roosting; chemical contaminants; fire regime; monitoring, capture, handling of the bats; tree and shrub vegetation; the vertebrate community; and water availability.

The CEM further proposes that these nine habitat elements, in turn, are directly shaped by six controlling factors included in the CEM. Specifically, the CEM proposes the following:

- Conservation monitoring and research programs shape the monitoring, capture, and handling of Townsend's big-eared bats within and immediately around the historic LCR floodplain, with proposed high magnitude and high understanding.

- Water storage-delivery system design and operation shape water availability across this landscape, with proposed high magnitude and high understanding.

- Fire management shapes the fire regime across this landscape, and nuisance species introduction and management and surrounding land use both shape the tree and shrub vegetation, with proposed high magnitude and medium understanding.

- Nuisance species introduction and management shapes the vertebrate community across this landscape, with proposed high magnitude and low understanding.

- Habitat development and management shapes the tree and shrub vegetation across this landscape, with proposed medium magnitude and medium understanding.

- Nuisance species introduction and management shapes the fire regime across this landscape, with proposed medium magnitude and low understanding.

- Surrounding land use shapes the distribution of chemical contaminants across this landscape, with proposed low magnitude and low understanding.

- Habitat development and management shapes the incidence of anthropogenic disturbance, nuisance species introduction and management shapes the arthropod community and the distribution of chemical contaminants, and surrounding land use shapes the arthropod and vertebrate communities and the incidence of anthropogenic disturbance across this landscape, with proposed unknown magnitude and low understanding.

Finally, the CEM proposes that several controlling factors affect each other in ways that ultimately affect foraging, commuting, night-roosting (interim roosting), and other critical biological activities or processes for Townsend's big-eared bats within and immediately around the historic LCR floodplain. Specifically, the CEM proposes the following:

- Conservation monitoring and research programs are affected by habitat development and management within and immediately around the historic LCR floodplain, with proposed high magnitude and high understanding.

- Nuisance species introduction and management across this landscape is affected by surrounding land use, and vice versa, with proposed high magnitude and medium understanding.

- Water storage-delivery system design and operation across this landscape is affected by habitat development and management, with proposed medium magnitude and high understanding.

- Fire management across this landscape is affected by surrounding land use, with proposed medium magnitude and medium understanding.

- Fire management and nuisance species introduction and management across this landscape are both affected by habitat development and management, with proposed unknown magnitude and low understanding.

- Nuisance species introduction and management across this landscape is affected by water storage-delivery system design and operation, with proposed unknown magnitude and low understanding.

Chapter 8 – Discussion and Conclusions

The proposed CEM for the Townsend's big-eared bat has several notable features. This chapter identifies and discusses these notable features.

First, there is a high level of uncertainty in the CEM. Tables 5 and 6 present general information on the causal relationships proposed in the CEM among the three life stages. The two tables together summarize the level of uncertainty present.

Table 5.—Proposed magnitudes of causal relationships in the CEM for Townsend's big-eared bats in the LCR ecosystem

Cause and effect node types		Proposed link magnitude				Row total
Causal node type	Effect node type	High	Medium	Low	Unknown	
Controlling factor	Controlling factor	4	11	0	6	**21**
Controlling factor	Habitat element	23	11	5	19	**58**
Habitat element	Habitat element	14	17	6	17	**54**
Habitat element	Activity or process	25	4	18	32	**79**
Activity or process	Habitat element	2	0	0	0	**2**
Activity or process	Activity or process	4	4	4	38	**50**
Activity or process	Life-stage outcome	12	0	4	21	**37**
Life-stage outcome	Activity or process	0	0	0	2	**2**
Life-stage outcome	Life-stage outcome	0	0	0	5	**5**
	Column total	**84**	**47**	**37**	**140**	**308**

Table 6.—Proposed level of understanding of causal relationships in the CEM for Townsend's big-eared bats in the LCR ecosystem

Cause and effect node types		Proposed link understanding			Row total
Causal node type	Effect node type	High	Medium	Low	
Controlling factor	Controlling factor	10	5	6	21
Controlling factor	Habitat element	16	9	33	58
Habitat element	Habitat element	9	9	36	54
Habitat element	Activity or process	8	16	55	79
Activity or process	Habitat element	2	0	0	2
Activity or process	Activity or process	0	0	50	50
Activity or process	Life-stage outcome	0	0	37	37
Life-stage outcome	Activity or process	0	0	2	2
Life-stage outcome	Life-stage outcome	0	0	5	5
	Column total	**45**	**39**	**224**	**308**

Table 5 shows that nearly half (140 out of 308) of all proposed causal links in the CEM were rated as having unknown magnitude. The CEM proposes links with unknown magnitude based on basic principles of bat biology and expectations articulated in the literature but for which no data or anecdotes are yet available for Townsend's big-eared bats or any similar or closely related species anywhere, let alone in the LCR ecosystem in particular. Further, causal links rated as having unknown magnitude comprise a much greater proportion of the links involving effects of life-stage outcomes (7 of 7) or effects of critical biological activities or processes (59 of 89) than of the links involving effects of habitat elements (49 of 133) or effects of controlling factors (25 of 79). This pattern reflects the lack of either anecdotes or formally collected evidence on many aspects of Townsend's big-eared bat biology and behavior that could help inform species or habitat management.

Similarly, table 6 shows that nearly three quarters (224 of 308) of all proposed links in the CEM were rated as having low understanding. Further, it is important to note that all 140 links with a proposed rating of unknown for magnitude necessarily also received a rating of low for understanding. A comparison of tables 5 and 6 therefore shows that half (84 of 168) of all links rated as having high, medium, or low magnitude were rated as having low understanding as well. The data in table 6 thus reflect a lack of either anecdotes or formally collected evidence on many aspects of Townsend's big-eared bat ecology or biology or behavior that could help inform species or habitat management.

Second, the assessment of causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes indicates the following strong (high-magnitude) causal relationships, regardless of link understanding:

- The CEM proposes that seven controlling factors have direct, high-magnitude effects on one or more habitat elements. These are, in alphabetical order: conservation monitoring and research programs; fire management; mining and mine management; nuisance species introduction and management; recreational use of caves and abandoned mines; surrounding land use; and water storage-delivery system design and operation. Two of these factors—mining and mine management and recreational use of caves and abandoned mines—concern only the uplands where Townsend's big-eared bats in the greater LCR ecosystem seek warm- and cold-season roosts. One of the remaining factors, water storage-delivery system design and operation, concerns only the historic LCR floodplain within the LCR MSCP planning area. The CEM assigns a rating of high and medium understanding to most of these high-magnitude effects of controlling factors on habitat elements. Chapters 4 and 5 discuss the sources of uncertainty for these causal relationships.

- The CEM proposes that seven habitat elements have direct, high-magnitude effects on one or more critical biological activities or processes in one or more life stages. These are, in alphabetical order: anthropogenic disturbance; arthropod community; caves and cave analogs; maternal care (a habitat element for pups but a critical biological activity or process for adult females); temperature; tree and shrub vegetation; and vertebrate community. The CEM assigns a rating of high and medium understanding to most of these high-magnitude effects of habitat elements on critical biological activities and processes. Two of these seven—maternal care (a habitat element for pups but a critical biological activity or process for adult females) and temperature—are relevant to only to the uplands where Townsend's big-eared bats in the greater LCR ecosystem seek warm- and cold-season roosts. The other five are relevant both to these uplands and to the historic LCR floodplain and its immediate vicinity—the zone that encompasses the LCR MSCP planning area. Chapters 3 and 4 discuss the sources of uncertainty for these causal relationships.

- The CEM proposes that six habitat elements have direct, high-magnitude effects on one or more other habitat elements and thereby have (or additionally have) strong indirect effects on one or more critical biological activities or processes in one or more life stages. These are, in alphabetical order: anthropogenic disturbance; arthropod community; caves and cave analogs; monitoring, capture, handling; temperature; and water availability. Four habitat elements thus have high-magnitude *direct and indirect* effects on one or more critical biological activities or processes among the three life stages: anthropogenic disturbance; arthropod community; caves and cave analogs; and temperature. The CEM assigns a rating of medium and low understanding to most of these high-magnitude effects of habitat elements on other habitat elements. The only two high-magnitude links between habitat elements with proposed ratings of high understanding are the linksbetween air temperature and fire regime, and between water availability and tree and shrub vegetation within the LCR planning area. Chapter 4 discusses the sources of uncertainty for these causal relationships.

- The CEM proposes that six critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes among the three life stages. These are, in alphabetical order: breeding, with proposed high-magnitude effects on adult fertility; chemical stress, with proposed high-magnitude effects on adult growth and survival; feeding, with proposed high-magnitude effects on pup growth and survival; foraging, with proposed high-magnitude effects on both juvenile and adult growth and survival; maternal care, with proposed high-magnitude effects on adult fertility; and predation, with proposed high-magnitude effects on juvenile and adult survival. The CEM assigns a rating of low understanding to all these high-magnitude effects of critical biological

activities or processes on life-stage outcomes. Three of these six—breeding, feeding, and maternal care—take place exclusively in the uplands where Townsend's big-eared bats in the greater LCR ecosystem seek warm- and cold-season roosts. Two of the other three—chemical stress and predation—are proposed to affect Townsend's big-eared bats in both the uplands and lowlands of the Lower Colorado River Valley. Only one of the six critical biological activities or processes with direct, high-magnitude effects on one or more life-stage outcomes, foraging, appears to take place exclusively in the historic LCR floodplain and its immediate vicinity. Chapter 3 discusses the sources of uncertainty for these causal relationships.

- The CEM proposes that three critical biological activities or processes have direct, high-magnitude effects on one or more other critical biological activities or processes. These three thereby have (or additionally have) strong indirect effects on one or more life-stage outcomes across the three life stages. These are, in alphabetical order: foraging, with proposed high-magnitude effects on breeding and maternal care, and both cold- and warm-season roosting, with proposed high-magnitude effects on breeding. The CEM assigns a rating of low understanding to all these high-magnitude effects of critical biological activities or processes on other critical biological activities or processes. Chapter 3 discusses the sources of uncertainty for these causal relationships.

The assessment of causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes also identifies numerous relationships with proposed intermediate (medium) and low magnitude. As knowledge about the species expands, the ratings of link magnitude for these proposed relationships, as well as for those currently assigned a high-magnitude rating, may change.

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ATTACHMENT 1

Species Conceptual Ecological Model Methodology for the Lower Colorado River Multi-Species Conservation Program

OVERVIEW OF METHODOLOGY

The conceptual ecological models (CEMs) for species covered by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) Habitat Conservation Plan expand on a methodology developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The ERP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and the National Marine Fisheries Service. The Bureau of Reclamation participates in this program.

The ERP methodology incorporates common best practices for constructing CEMs for individual species (DiGennaro et al. 2012; Fischenich 2008; Wildhaber et al. 2007, 2011). It has the following key features:

- It focuses on the *major life stages or events* through which each species passes and the *output(s)* of each life stage or event. Outputs typically consist of survivorship or the production of offspring.

- It identifies the *major drivers* that affect the likelihood (rate) of each output. Drivers are physical, chemical, or biological factors—both natural and anthropogenic—that affect output rates and, therefore, control the viability of the species in a given ecosystem.

- It characterizes these interrelationships using a "*driver-linkage-outcomes*" approach. Outcomes are the output rates. Linkages are cause-effect relationships between drivers and outcomes.

- It *characterizes each causal linkage* along four dimensions: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the certainty of present scientific understanding of the effect (DiGennaro et al. 2012).

The CEM methodology used for species covered by the LCR MSCP Habitat Conservation Plan species expands this ERP methodology. Specifically, the present methodology incorporates the recommendations and examples of Burke et al. (2009), Kondolf et al. (2008), and Wildhaber et al. (2007, 2011) for a more hierarchical approach and adds explicit demographic notation for the characterization of life-stage outcomes (McDonald and Caswell 1993). This expanded approach provides greater detail on causal linkages and outcomes. The expansion specifically calls for identifying **four** types of model components for each life stage, and the causal linkages among them, as follows:

- **Life-stage outcomes** are outcomes of an individual life stage, including the recruitment of individuals to the next succeeding life stage (e.g., juvenile to adult). For some life stages, the outcomes, alternatively or additionally, may include the survival of individuals to an older age class within the same life stage or the production of offspring. The rates of life-stage outcomes depend on the rates of the critical biological activities and processes for that life stage.

- **Critical biological activities and processes** are activities in which a species engages and the biological processes that must take place during each life stage that significantly affect life-stage outcomes. They include activities and processes that may benefit or degrade life-stage outcomes. Examples of critical biological activities and processes include mating, foraging, avoiding predators, avoiding other specific hazards, gamete production, egg maturation, leaf production, and seed germination. Critical biological activities and processes are "rate" variables. Taken together, the rate (intensity) of these activities and processes determine the rates of different life-stage outcomes.

- **Habitat elements** are specific habitat conditions that significantly ensure, allow, or interfere with critical biological activities and processes. The full suite of natural habitat elements constitutes the natural habitat template for a given life stage. Human activities may introduce habitat elements not present in the natural habitat template. Defining a habitat element may involve estimating the specific ranges of quantifiable properties of that element *whenever the state of knowledge supports such estimates*. These properties concern the abundance, spatial and temporal distributions, and other qualities of the habitat element that significantly affect the ways in which it ensures, allows, or interferes with critical biological activities and processes.

- **Controlling factors** are environmental conditions and dynamics—both natural and anthropogenic—that determine the quality, abundance, and spatial and temporal distributions of one or more habitat elements. In some instances, a controlling factor alternatively or additionally may directly affect a critical biological activity or process. Controlling factors are also called "drivers." A hierarchy of controlling factors will exist, affecting the system at different temporal and spatial scales. Long-term dynamics of climate and geology define the domain of this hierarchy (Burke et al. 2009). For example, the availability of suitable nest sites for a riparian nesting bird may depend on factors such as canopy closure, community type, humidity, and intermediate structure which, in turn, may depend on factors such as water storage-delivery system design and operation (dam design, reservoir morphology, and dam operations) which, in turn, is shaped by watershed geology, vegetation, climate, land use, and

water demand. *The LCR MSCP conceptual ecological models focus on controlling factors that are within the scope of potential human manipulation, including management actions directed toward the species of interest.*

This CEM methodology also explicitly defines a "life stage" as a biologically distinct portion of the life cycle of a species. The individuals in each life stage undergo distinct developments in body form and function; engage in distinct types behaviors, including reproduction; use different sets of habitats or the same habitats in different ways; interact differently with their larger ecosystems; and/or experience different types and sources of stress. A single life stage may include multiple age classes. A CEM focused on life stages is not a demographic model per se (McDonald and Caswell 1993); instead, it is a complementary model focused on the ecological factors (drivers) that shape population dynamics.

This expanded approach permits the consideration of **six** possible types of causal relationships, on which management actions may focus, for each life stage of a species:

(1) The effect of one controlling factor on another

(2) The effect of a controlling factor on the abundance, spatial and temporal distributions, and other qualities of a habitat element

(3) The effect of the abundance, spatial and temporal distributions, and other qualities of one habitat element on those of another

(4) The effect of the abundance, spatial and temporal distributions, and other qualities of a habitat element on a critical biological activity or process

(5) The effect of one critical biological activity or process on another

(6) The effect of a critical biological activity or process on a specific life-stage outcome

Each controlling factor may affect the abundance, spatial and temporal distributions, and other qualities of more than one habitat element, and several controlling factors may affect the abundance, spatial or temporal distributions, or other qualities of each habitat element. Similarly, the abundance, spatial and temporal distributions, and other qualities of each habitat element may affect more than one biological activity or process, and the abundances, spatial or temporal distributions, or other qualities of several habitat elements may affect each biological activity or process. Finally, the rate of each critical biological activity or process may contribute to the rates of more than one life-stage outcome.

Integrating this information across all life stages for a species provides a detailed picture of: (1) what is known, with what certainty, and the sources of this information, (2) critical areas of uncertain or conflicting science that demand resolution to better guide LCR MSCP management planning and action, (3) crucial attributes to use to monitor system conditions and predict the effects of experiments, management actions, and other potential agents of change, and (4) how managers may expect the characteristics of a resource to change as a result of changes to controlling factors, including changes in management actions.

Conceptual Ecological Models as Hypotheses

The CEM for each species produced with this methodology constitutes a collection of hypotheses for that species. These hypotheses concern: (1) the species' life history, (2) the species' habitat requirements and constraints, (3) the factors that control the quality, abundance, and spatial and temporal distributions of these habitat conditions, and (4) the causal relationships among these. Knowledge about these model components and relationships may vary, ranging from well settled to very tentative. Such variation in the certainty of current knowledge always arises as a consequence of variation in the types and amount of evidence available and in the ecological assumptions applied by different experts.

Wherever possible, the information assembled for the LCR MSCP species CEMs documents the degree of certainty of current knowledge concerning each component and linkage in the model. This certainty is indicated by the quality, abundance, and consistency of the available evidence and by the degree of agreement/disagreement among the experts. Differences in the interpretations or arguments offered by different experts may be represented as alternative hypotheses. Categorizing the degree of agreement/disagreement concerning the components and linkages in a CEM makes it easier to identify topics of greater uncertainty or controversy.

Characterizing Causal Relationships

A causal relationship exists when a change in one condition or property of a system results in a change in some other condition or property. A change in the first condition is said to cause a change in the second condition. This CEM methodology includes methods for assessing causal relationships (links) along four dimensions (attributes) adapted from the ERP methodology (DiGennaro et al. 2012):

(1) The character and direction of the effect

(2) The magnitude of the effect

(3) The predictability (consistency) of the effect

(4) The certainty of present scientific understanding of the effect

The present and ERP methodologies for assessing causal linkages differ in three ways. First, the ERP methodology assesses these four attributes for the *cumulative* effect of the entire causal chain leading up to each outcome. However, the LCR MSCP methodology recognizes six different types of causal linkages as described above. This added level of detail and complexity makes it difficult, in a single step, to assess the cumulative effects of all causal relationships that lead up to any one individual causal link. For example, in the present methodology, the effect of a given critical biological activity or process on a particular life-stage outcome may depend on the effects of several habitat elements on that critical biological activity or process which, in turn, may depend on the effects of several controlling factors. For this reason, the present methodology assesses the four attributes separately for each causal link *by itself* rather than attempting to assess cumulative effects of all causal linkages leading to the linkage of interest. The present methodology assesses cumulative effects instead through analyses of the data assembled on all individual linkages. The analyses are made possible by assembling the data on all individual linkages in a spreadsheet as described below.

Second, the CEM methodology explicitly divides link magnitude into three separate subattributes and provides a specific methodology for integrating their rankings into an overall ranking for link magnitude: (1) link intensity, (2) link spatial scale, and (3) link temporal scale. In contrast, the ERP methodology treats spatial and temporal scale together and does not separately evaluate link intensity. The present methodology defines link intensity as the relative strength of the effect of the causal node on the affected node *at the places and times where the effect occurs*. Link spatial scale is the relative spatial extent of the effect of the causal node on the affected node. Link temporal scale is the relative temporal extent of the effect of the causal node on the affected node. The present methodology defines link magnitude as the average of the separate rankings of link intensity, spatial scale, and temporal scale as described below.

Third, the ERP methodology addresses a single, large landscape, while the present methodology needed the flexibility to generate models applicable to a variety of spatial scopes. For example, the present methodology needed to support modeling of a single restoration site, the LCR main stem and floodplain, or the entire Lower Colorado River Basin. Consequently, the present methodology assesses the spatial scale of cause-effect relationships only relative to the spatial scope of the model.

The LCR MSCP conceptual ecological model methodology thus defines the four attributes for a causal link as follows:

- **Link character** – This attribute categorizes a causal relationship as positive, negative, involving a threshold response, or "complex." "Positive" means that an increase in the causal node results in an increase in the affected node, while a decrease in the causal node results in a decrease in the affected node. "Negative" means that an increase in the causal node results in a decrease in the affected element, while a decrease in the causal node results in an increase in the affected node. Thus, "positive" or "negative" here do ***not*** mean that a relationship is beneficial or detrimental. The terms instead provide information analogous to the sign of a correlation coefficient. "Threshold" means that a change in the causal agent must cross some value before producing an effect. "Complex" means that there is more going on than a simple positive, negative, or threshold effect. In addition, this attribute categorizes a causal relationship as uni- or bi-directional. Bi-directional relationships involve a reciprocal relationship in which each node affects the other.

- **Link magnitude** – This attribute refers to "… the degree to which a linkage controls the outcome *relative to other drivers*" (DiGennaro et al. 2012). Magnitude takes into account the spatial and temporal scale of the causal relationship as well as the strength (intensity) of the relationship in individual locations. The present methodology provides separate ratings for the intensity, spatial scale, and temporal scale of each link, as defined above, and assesses overall link magnitude by averaging these three elements. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link magnitude provide information analogous to the size of a correlation coefficient. Tables 1-1 through 1-4 (at the end of this attachment) present the rating framework for link magnitude.

- **Link predictability** – This attribute refers to "… the degree to which the current understanding of the system can be used to predict the role of the driver in influencing the outcome. Predictability … captures variability … [and recognizes that] effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult" (DiGennaro et al. 2012). A causal relationship may be unpredictable because of natural variability in the system or because its effects depend on the interaction of other factors with independent sources for their own variability. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link predictability provide information analogous to the size of the range of error for a correlation coefficient. Table 1-5 presents the scoring framework for link predictability.

- **Link understanding** refers to the degree of agreement represented in the scientific literature and among experts in understanding how each driver is linked to each outcome. Table 1-6 presents the scoring framework for understanding. Link predictability and understanding are independent attributes. A link may be considered highly predictable but poorly understood or poorly predictable but well understood.

Conceptual Ecological Model Documentation

The documentation for each CEM provides information in three forms: (1) a narrative report, (2) causal diagrams showing the model components and their causal linkages for each life stage, and (3) a spreadsheet that is used to record the detailed information (e.g., linkage attribute ratings) for each causal linkage. The spreadsheet and diagrams, built using Microsoft Excel™ and Microsoft Visio™, respectively, are linked so that the diagrams provide a fully synchronized summary of the information in the spreadsheet. This linkage between the two applications, supported by software scripts developed in association with these CEMs, allow users to generate a "master" diagram for each life stage from the data in the spreadsheet and, crucially, to query the CEM spreadsheet for each life stage and generate diagrams that selectively display query results concerning that life stage.

The narrative report for each species presents the definitions and rationales for the life stages/events and their outcomes identified for the species' life history; the critical biological activities and processes identified for each life stage; the habitat elements identified as supporting or impeding each critical biological activity or process for each life stage; the controlling factors identified as affecting the abundance, spatial and temporal distributions, and other qualities of the habitat elements for each life stage; and the causal linkages among these model components.

The narrative report includes causal diagrams (*aka* "influence diagrams") for each life stage. These diagrams show the individual components or nodes of the model for that stage (life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors) and their causal relationships. The causal relationships (causal links) are represented by arrows indicating which nodes are linked and the directions of the causal relationships. The attributes of each causal link are represented by varying line thickness, line color, and other visual properties as shown on figure 1-1. The diagram conventions mostly follow those in the ERP methodology (DiGennaro et al. 2012).

The spreadsheet for each CEM contains a separate worksheet for each life stage. Each row in the worksheet for a life stage represents a single causal link. Table 1-7 lists the fields (columns) recorded for each causal link.

Link Attribute Ratings, Spreadsheet Fields, and Diagram Conventions

Table 1-1.—Criteria for rating the relative intensity of a causal relationship – one of three variables in the rating of link magnitude (after DiGennaro et al. 2012, Table 2)

Link intensity – the relative strength of the effect of the causal node on the affected node *at the places and times where the effect occurs*.	
High	Even a relatively small change in the causal node will result in a relatively large change in the affected node *at the places and times where the effect occurs*.
Medium	A relatively large change in the causal node will result in a relatively large change in the affected node; a relatively moderate change in the causal node will result in no more than a relatively moderate change in the affected node; and a relatively small change in the causal node will result in no more than a relatively small change in the affected node *at the places and times where the effect occurs*.
Low	Even a relatively large change in the causal node will result in only a relatively small change in the affected node *at the places and times where the effect occurs*.
Unknown	Insufficient information exists to rate link intensity.

Table 1-2.—Criteria for rating the relative spatial scale of a cause-effect relationship – one of three variables in the rating of link magnitude (after DiGennaro et al. 2012, Table 1)

Link spatial scale – the relative spatial extent of the effect of the causal node on the affected node. The rating takes into account the spatial scale of the cause and its effect.	
Large	Even a relatively small change in the causal node will result in a change in the affected node across a large fraction of the spatial scope of the model.
Medium	A relatively large change in the causal node will result in a change in the affected node across a large fraction of the spatial scope of the model; a relatively moderate change in the causal node will result in a change in the affected node across no more than a moderate fraction of the spatial scope of the model; and a relatively small change in the causal node will result in a change in the affected node across no more than a small fraction of the spatial scope of the model.
Small	Even a relatively large change in the causal node will result in a change in the affected node across only a small fraction of the spatial scope of the model.
Unknown	Insufficient information exists to rate link spatial scale.

Table 1-3.—Criteria for rating the relative temporal scale of a cause-effect relationship – one of three variables in the rating of link magnitude (after DiGennaro et al. 2012, Table 1)

Link temporal scale – the relative temporal extent of the effect of the causal node on the affected node. The rating takes into account the temporal scale of the cause and its effect.	
Large	Even a relatively small change in the causal node will result in a change in the affected node that persists or recurs over a relatively large span of time—decades or longer—even without specific intervention to sustain the effect.
Medium	A relatively large change in the causal node will result in a change in the affected node that persists or recurs over a relatively large span of time—decades or longer—even without specific intervention to sustain the effect; a relatively moderate change in the causal node will result in a change in the affected node that persists or recurs over only a relatively moderate span of time—one or two decades—without specific intervention to sustain the effect; a relatively small change in the causal node will result in a change in the affected node that persists or recurs over only a relatively short span of time—less than a decade—without specific intervention to sustain the effect.
Small	Even a relatively large change in the causal node will result in a change in the affected node that persists or recurs over only a relatively short span of time—less than a decade—without specific intervention to sustain the effect.
Unknown	Insufficient information exists to rate link temporal scale.

Table 1-4.—Criteria for rating the overall relative link magnitude of a cause-effect relationship based on link intensity, spatial scale, and temporal scale

Link magnitude – the overall relative magnitude of the effect of the causal node on the affected node based on the numerical average for link intensity, spatial scale, and temporal scale. (Calculated by assigning a numerical value of 3 to "High" or "Large," 2 to "Medium," 1 to "Low" or "Small," and not counting missing or "Unknown" ratings.)	
High	Numerical average ≥ 2.67
Medium	Numerical average ≥ 1.67 but < 2.67
Low	Numerical average < 1.67
Unknown	No subattribute is rated High/Large, Medium, or Low/Small, but at least one subattribute is rated Unknown.

Table 1-5.—Criteria for rating the relative predictability of a cause-effect relationship (after DiGennaro et al. 2012, Table 3)

Link predictability – the statistical likelihood that a given causal agent will produce the effect of interest.	
High	Magnitude of effect is largely unaffected by random variation or by variability in other ecosystem dynamics or external factors.
Medium	Magnitude of effect is moderately affected by random variation or by variability in other ecosystem processes or external factors.
Low	Magnitude of effect is strongly affected by random variation or by variability in other ecosystem processes or external factors.
Unknown	Insufficient information exists to rate link predictability.

Table 1-6.—Criteria for rating the relative understanding of a cause-effect relationship (after DiGennaro et al. 2012, Table 3)

Understanding – the degree of agreement in the literature and among experts on the magnitude and predictability of the cause-effect relationship of interest.	
High	Understanding of the relationship is subject to little or no disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern or in scientific reasoning among experts familiar with the ecosystem. Understanding may also rest on well-accepted scientific principles and/or studies in highly analogous systems.
Medium	Understanding of the relationship is subject to moderate disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.
Low	Understanding of the relationship is subject to wide disagreement, uncertainty, or lack of evidence in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.
Unknown	(*The "Low" rank includes this condition*).

Table 1-7.—Organization of the worksheet for each life stage

Col.	Label	Content
A	Species	Identifies the species being modeled by four-letter code.
B	Link#	Contains a unique identification number for each causal link.
C	Life Stage	Identifies the life stage affected by the link.
D	Causal Node Type	Identifies whether the causal node for the link is a controlling factor, habitat element, critical biological activity or process, or life-stage outcome.
E	Causal Node	Identifies the causal node in the link.
F	Effect Node Type	Identifies whether the effect node for the link is a controlling factor, habitat element, critical biological activity or process, or life-stage outcome.
G	Effect Node	Identifies the effect node in the link.
H	Link Reason	States the rationale for including the link in the CEM, including citations as appropriate.
I	Link Character Type	Identifies the character of the link based on standard definitions.
J	Link Character Direction	Identifies whether the link is uni- or bi-directional.
K	Link Character Reason	States the rationale for the entries for Link Character Type and Link Character Direction, including citations as appropriate.
L	Link Intensity	Shows the rating of link intensity based on the definitions in table 1-1.
M	Link Spatial Scale	Shows the rating of link spatial scale based on the definitions in table 1-2.
N	Link Temporal Scale	Shows the rating of link temporal scale based on the definitions in table 1-3.
O	Link Average Magnitude	Shows the numerical average rating of link intensity, spatial scale, and temporal scale based on the definitions in table 1-4.
P	Link Magnitude Rank	Shows the overall rating of link magnitude based on the Link Average Magnitude, grouped following the criteria in table 1-4.
Q	Link Magnitude Reason	States the rationale for the ratings for link intensity, spatial scale, and temporal scale, with citations as appropriate.
R	Link Predictability Rank	Shows the rating of link predictability based on the definitions in table 1-5.
S	Link Predictability Reason	States the rationale for the rating of link predictability, with citations as appropriate.
T	Link Understanding Rank	Shows the rating of link understanding based on the definitions in table 1-6.
U	Link Understanding Reason	States the rationale for the rating of link predictability, including comments on alternative interpretations and publications/experts associated with different interpretations when feasible, with citations as appropriate.
V	Management Questions	Briefly notes questions that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in knowledge concerning *management actions and options*, with reasoning, including the estimate of relative importance when possible.
W	Research Questions	Brief notes that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in *basic scientific knowledge*, with reasoning, including the estimate of relative importance when possible.
X	Other Comments	Provides additional notes on investigator concerns, uncertainties, and questions.
Y	Update Status	Provides information on the history of editing the information on this link for updates carried out after completion of an initial version.

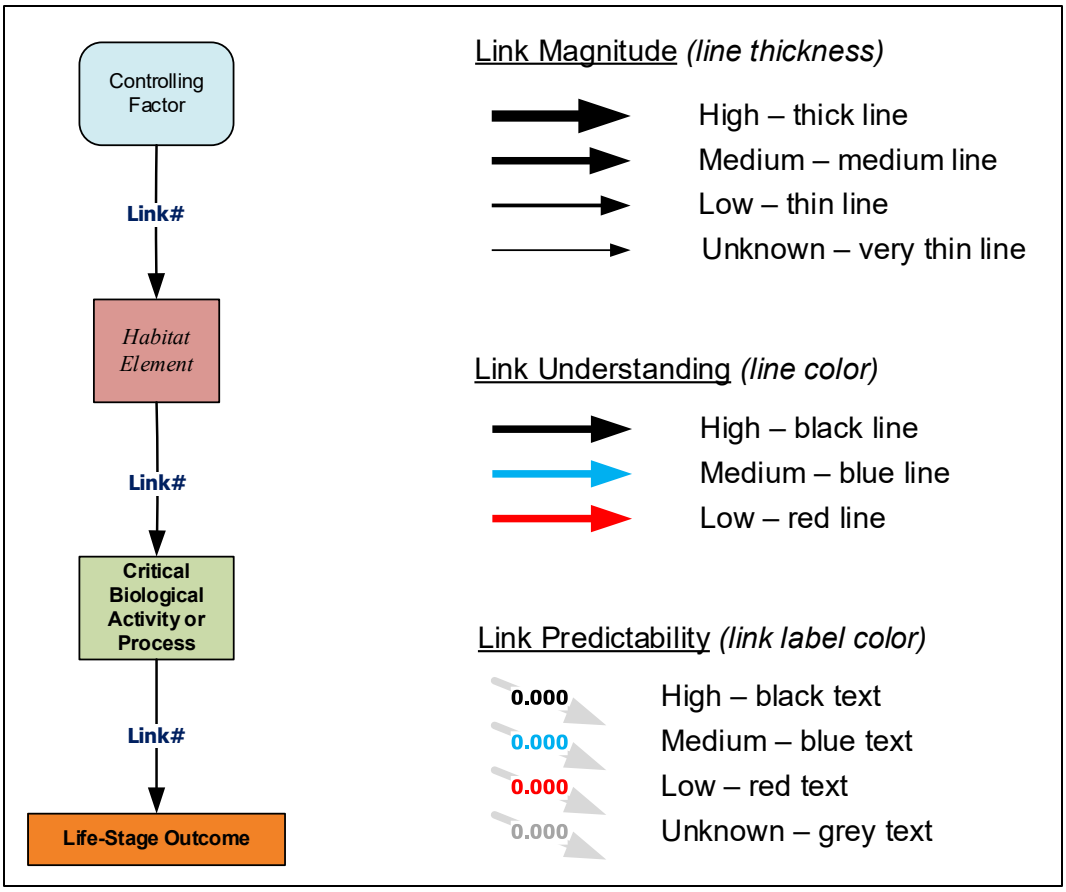

Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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