



Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

California Leaf-nosed Bat (*Macrotus californicus*) (CLNB) Basic Conceptual Ecological Model for the Lower Colorado River

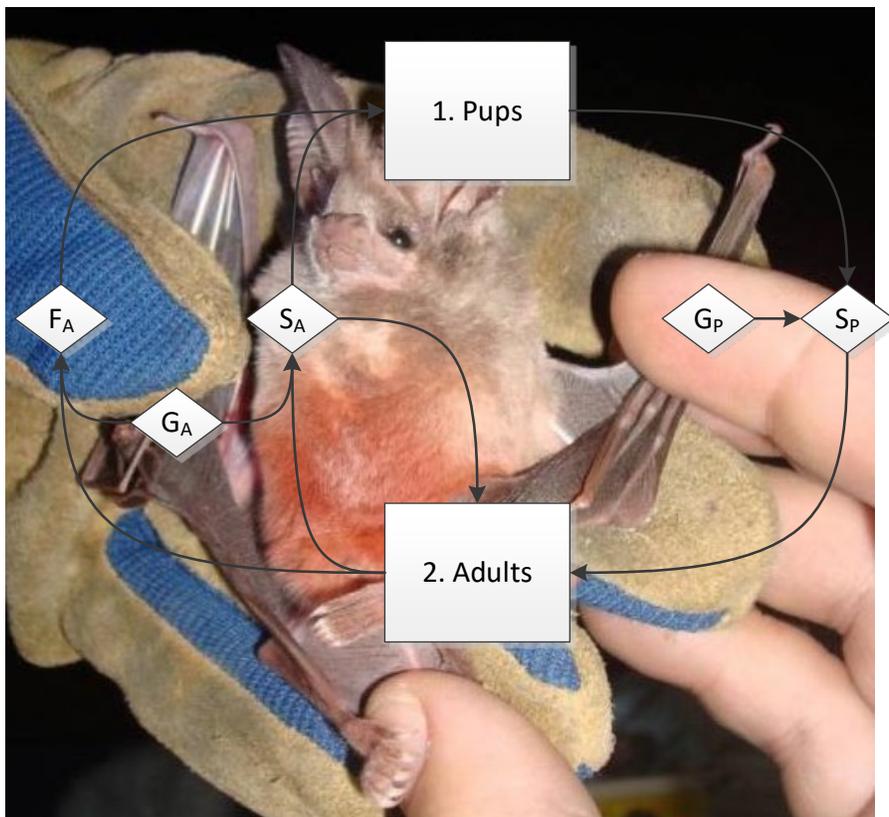


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May 2020

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Lower Colorado River Multi-Species Conservation Program

California Leaf-nosed bat (*Macrotus californicus*) (CLNB) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

AZGFD	Arizona Game and Fish Department
CEM	conceptual ecological model
CLNB	California leaf-nosed bat (<i>Macrotus californicus</i>)
CRTR	Colorado River Terrestrial and Riparian
DNA	deoxyribonucleic acid
ERP	Sacramento-San Joaquin Delta Ecosystem Restoration Program
HCP	Habitat Conservation Plan
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
mtDNA	mitochondrial deoxyribonucleic acid
km	kilometer(s)
Reclamation	Bureau of Reclamation
USFWS	U.S. Fish and Wildlife Service

Symbols

°C	degrees Celsius
°F	degrees Fahrenheit
>	greater than
≥	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.

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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. 2003¹). 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. 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.

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, the 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 California leaf-nosed bat (*Macrotus californicus*) (CLNB). The CLNB is 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 (LCR MSCP 2004).

The purpose of this CEM is to help the LCR MSCP identify areas of scientific uncertainty concerning (1) CLNB ecology, (2) the effects of specific stressors, (3) the effects of management actions aimed at habitat restoration, and (4) the methods used to measure CLNB 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.)

The CEM addresses the overall landscape used by CLNB along the Lower Colorado River Valley, not just the portions that lie within the LCR MSCP planning area. However, the CEM also captures the reality that the life cycle of CLNB in the greater lower Colorado River (LCR) ecosystem plays out in two distinct settings: their cold- and warm-season roosting sites, which in this ecosystem occur exclusively in uplands; and their foraging habitat, which consists of upland washes and the lowlands of the historic LCR floodplain and its immediate vicinity. LCR MSCP management responsibilities lie within its planning area, in cooperation with other Federal agencies, States, and Tribes. This planning area encompasses only a few areas of upland. 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 CLNB 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 methodology 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 CEM 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

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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 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 to generate diagrams that selectively display query results concerning the CEM for each life stage.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The CLNB conceptual ecological model rests on the most recent comprehensive reviews of the literature for CLNB (Arizona Game and Fish Department 2014; Brown 2013; LCR MSCP 2016; NatureServe 2019; O’Shea et al. 2018; Western Bat Working Group 2019), along with the findings of studies (Elliott et al. 2017; Tobin and Chambers 2017) that these five reviews mostly do not address, including the findings of field investigations in the Lower Colorado River Valley by and for the LCR MSCP over the past roughly 15 years (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Brown 2006, 2010, 2013, *in press*;

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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; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010).

The CLNB conceptual ecological model also incorporates the expert knowledge of LCR MSCP biologists, the results of genetic studies of CLNB centered on the Lower Colorado River Valley (Hill 2011, 2016, 2019a), and information presented at the annual Colorado River Terrestrial and Riparian meetings in 2014–17 (Broderick 2014; Brown 2015; Brown and Rainey 2016; Calvert 2014, 2015, 2016c, 2017; Mixan 2015, 2016, 2017; Mixan and Diamond 2014b; Rubin et al. 2014). Finally, the CEM incorporates information on bat ecology and conservation in general from numerous sources, including Bunkley et al. (2015), Mikula (2015), and Mikula et al. (2016), and information on rabies transmission and effects in CLNB from Stuchin et al. (2018). However, the purpose of the present 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.

The CLNB conceptual ecological model for the greater LCR ecosystem identifies two life stages based on the aforementioned sources of information, and two or more life-stage outcomes for each life stage, as follows:

- Pup life stage: pup growth, pup survival
- Adult life stage: adult growth, adult survival, adult fertility

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

The CEM identifies 15 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 15 critical biological activities and processes are as follows, in alphabetical order: breeding; chemical stress; competition; disease; drinking; feeding; foraging; inter-site movement; maternal care (a critical biological activity or process for adults but a habitat element for pups); mechanical stress; predation; roosting: cold season; roosting: warm season; roosting: interim; and thermal stress. The reasoning for including these 15 critical biological activities and processes parallels the reasoning recently applied to CEMs for 3 other bat species in the Lower Colorado River Valley: western red bats (*Lasiurus blossevillii*), western yellow bats (*Lasiurus xanthinus* = *Dasypterus xanthinus*), and Townsend's big-eared bats (*Corynorhinus townsendii*) (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

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or processes for 1 or both 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 (a habitat element for pups but a critical biological activity or process for adults); 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 Townsend's big-eared 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 underground 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 Townsend's big-eared bats (Braun and Unnasch 2020a, 2020b, 2020c).

RESULTS

Approximately 30% (69 of 227) of all proposed causal links in the CEM, across both life stages combined, 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 CLNB 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 critical biological activities or processes (46 of 71) than of the links involving effects of life-stage outcomes (2 of 6), habitat elements (14 of 89), or controlling factors (17 of 61). This pattern reflects a lack of either anecdotes or formally collected evidence on several aspects of CLNB biology and behavior that could help guide species or habitat management.

In turn, more than 70% (160 of 227) of all proposed links in the CEM, across both life stages combined, were rated as having low understanding. Further, it is important to note that all 69 links with a proposed rating of unknown for

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magnitude necessarily also received a rating of low for understanding. A comparison of tables 5 and 6 therefore shows that nearly 58% (91 of 158) 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 more strongly indicates a lack of either anecdotes or formally collected evidence on many aspects of CLNB 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. The seven controlling factors are as follows, 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—mostly concern only the uplands where CLNB in the greater LCR ecosystem seek cold- and warm-season roosts outside the LCR MSCP planning area. However, a few mines lie within the planning area. 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 low understanding to several (6 of 16) 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 seven habitat elements are as follows, 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 fewer than half (8 of 18) of these high-magnitude effects of habitat elements on critical biological activities and processes. One of these seven, maternal care (a habitat element for pups but a critical biological activity or process for adult females), is relevant to only to the uplands where CLNB in the greater LCR ecosystem find most of their cold- and warm-season roosts. The other six 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.

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- 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. The six habitat elements are as follows, in alphabetical order: anthropogenic disturbance; caves and cave analogs; chemical contaminants; monitoring, capture, handling; temperature; and water availability. Three habitat elements thus have high-magnitude *direct and indirect* effects on one or more critical biological activities or processes across the two life stages: arthropod community, caves and cave analogs, and temperature. The CEM assigns a rating of medium and low understanding to most (10 of 15) of the high-magnitude effects of habitat elements on other habitat elements. The five high-magnitude links between habitat elements with proposed ratings of high understanding are between monitoring and anthropogenic disturbance (directly affects both pup and adult life stages), between air temperature and the fire regime (directly affects both pup and adult life stages), and between water availability and the tree and shrub vegetation within the LCR planning area (directly affects only the adult life stage). Chapter 4 discusses the sources of uncertainty for these causal relationships.

- The CEM proposes that four critical biological activities and processes in the adult life stage reciprocally affect one habitat element—monitoring, capture, handling—with medium to high magnitude. (1) CLNB adult foraging behaviors constrain the ability of investigators to detect and distinguish their echolocation calls using acoustic monitoring equipment or to capture them in mist nets in different settings, for several reasons discussed in chapter 4 (see “Monitoring, Capture, Handling”). The CEM rates this link as having high magnitude and moderate understanding. (2) CLNB cold- and warm-season roosting behaviors, including roosting site selection, also can constrain the ability of investigators to observe and count CLNB as they exit and enter their roosting sites. The CEM rates these two links as having medium magnitude and moderate understanding. (3) CLNB drinking behaviors appear to limit the ability of investigators to capture them in mist nets over water. The CEM rates this link as having high magnitude but low understanding. The CEM thus indicates that a combination of CLNB behaviors and abilities may limit the ability of investigators to determine where and how often the bats forage, and how they behave while foraging, particularly how they orient themselves to and patrol in and around vegetation patches and openings, and how many CLNB use different foraging areas and daytime roosting sites. Another monitoring method, the tracking of individual CLNB using radio tags, has provided useful information on overall foraging ranges and routes; however, such tracking has involved only a small number of individuals and does not provide a high level of detail for studying behaviors in and around individual foraging areas.

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- The CEM proposes that seven critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes across the two life stages. The seven critical biological activities or process are as follows, in alphabetical order: breeding, with proposed high-magnitude effects on adult fertility; chemical stress, with proposed high-magnitude effects on both pup and adult growth and survival; feeding, with proposed high-magnitude effects on pup growth and survival; foraging, with proposed high-magnitude effects on adult growth and survival; maternal care, with proposed high-magnitude effects on adult fertility; predation, with proposed high-magnitude effects on adult survival; and thermal stress, with proposed high-magnitude effects on both pup and adult growth and 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 seven—breeding, feeding, and maternal care—take place exclusively in the uplands where CLNB in the greater LCR ecosystem seek cold- and warm-season roosts. Three of the other four—chemical stress, predation, and thermal stress—are proposed to affect CLNB in both the uplands and lowlands of the Lower Colorado River Valley. Only one of the seven—foraging—appears to take place mostly across the lowlands comprising the historic LCR floodplain and its immediate vicinity. Chapter 3 discusses the sources of uncertainty for these causal relationships.
- The CEM proposes that four critical biological activities or processes have direct, high-magnitude effects on one or more other critical biological activities or processes. These four thereby have (or additionally have) strong indirect effects on one or more life-stage outcomes across the two CLNB life stages. The four critical biological activities or processes are as follows, in alphabetical order: drinking, with proposed high-magnitude effects on chemical stress; foraging, with proposed high-magnitude effects on breeding, drinking, and maternal care; and both cold- and warm-season roosting, with proposed high-magnitude effects on breeding. The CEM assigns a rating of high understanding to the relationship between warm-season roosting and breeding, ratings of medium understanding to the relationships between drinking and chemical stress and between foraging and drinking, and ratings of low understanding to the relationships between foraging and both breeding and maternal care, and between cold-season roosting and breeding. 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.

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for the California leaf-nosed bat (*Macrotus californicus*) (CLNB). The CLNB bat is 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 (LCR MSCP 2004).

The purpose of this CEM is to help the LCR MSCP identify areas of scientific uncertainty concerning CLNB ecology, the effects of specific stressors, the effects of management actions aimed at habitat restoration, and the methods used to measure CLNB 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.)

The historic range of CLNB included and, within the United States portion of this range, centered on the Lower Colorado River Valley (Arizona Game and Fish Department [AZGFD] 2014; O’Shea et al. 2018). The LCR MSCP (2016) states:

The historical range of California leaf-nosed bats included records from San Diego and Riverside Counties, California, eastward to Tombstone, Arizona, and south into Baja California and Sonora, Mexico, with the center of their distribution appearing to be the location of their first recorded description at Fort Yuma, California, opposite Yuma, Arizona (Grinnell 1914). Hatfield (1937) found leaf-nosed bats at a winter night roost east of Searchlight, Nevada, and Cockrum and Musgrove (1964) found a large roost in a mine 4.5 miles north of Davis Dam and 0.75 mile west of Lake Mojave. At least three mines that were known roost sites were inundated by water with the formation of Lakes Mead and Mojave (O’Farrell 1970).

Brown (*in press*) summarizes the current distribution of CLNB roosting sites along the greater Lower Colorado River Valley as follows (see also AZGFD 2019; Brown 2013):

Extensive surveys conducted over the past 40 years indicate that the species now appears to be limited to the eastern portion of its former range in California (Brown and Berry 1998 and 2004), and the largest colonies are found in the mountain ranges bordering the Colorado River basin... Stager (1939) and

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*Vaughan (1959) found California leaf-nosed bats to be one of the most common bats in the mines of the Riverside Mountains, and this is still the case (Brown and Berry 1998). During their survey of all mines on the Arizona side of the Imperial NWR [National Wildlife Refuge], AZGFD [Arizona Game and Fish Department] biologists (Castner et al. 1995) located California leaf-nosed bats roosting in 14 mines in addition to the Eureka Mine. Currently, six major (> 100 bats) maternity colonies occur in mines near the LCR (Senator, Roosevelt, Rio Vista, Morningstar, Steece, and Californian, with smaller colonies in the Alice, Eureka, Islander and Golden Dream). The maternity colony in the Golden Dream Mine has declined considerably in the past 6 years. At least seven mines up the Bill Williams River contain colonies of 100 to 1,000 *Macrotus* (Brown 1996). Five of these mines are in the Planet Mine area. Larger winter roosts (> 300 bats) occur in only eight mines along the LCR (3C, Hart, Stonehouse, Steece, Mountaineer, Alice, Californian, and Jackpot, with smaller colonies in the Roosevelt, Rio Vista, Senator, Islander and Homestake) as well as several along the Bill Williams River, two of which are located in the Planet Mine area. The largest colony of over 4,000 bats inhabits the Stonehouse Mine complex, followed in numbers by the Hart and 3C Mines.*

CLNB roost in these mines during either the cold season, warm season, or both. Spatially, the mine locations extend north-to-south along the greater Lower Colorado River Valley from the Homestake Mine near Laughlin, Nevada, to the 3C Mine near Yuma, Arizona. The majority of these mines, including the five mines in the Planet Mines area of the Bill Williams River valley in Arizona, lie within or very close to the margins of the LCR MSCP planning area. However, several lie five or more kilometers (km) beyond the limits of this planning area, including the Alice, Steece, and Mountaineer Mines in the Riverside Mountains, California, and the Stonehouse and Roosevelt Mines in the Mule Mountains, California. However, telemetry studies (Brown 2010, 2013, 2015, 2016, *in press*; Brown and Rainey 2016; Maturango Museum and Brown-Berry Biological Consulting 2018) and more extensive acoustic monitoring efforts (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Diamond 2012; Diamond et al. 2013; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2012, 2013; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010) indicate that the CLNB along the greater Lower Colorado River Valley forage not only along washes that drain onto the historic LCR floodplain but also extensively across the floodplain, including LCR MSCP conservation areas and other habitat creation areas, in the vicinities of which the bats also may use interim roosting sites for night feeding. Their commuting routes and their zone of foraging and night roosting loosely encompass the LCR MSCP planning area. The LCR MSCP therefore recognizes the CLNB that use the planning area as an LCR population.

This CEM addresses the overall landscape used by the species along the greater Lower Colorado River Valley, not just the portions that lie within the LCR MSCP planning area. However, the CEM also recognizes that the life cycle of CLNB in

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the greater Lower Colorado River Valley plays out in two distinct settings: their cold- and warm-season roosting sites, which in this ecosystem occur exclusively in uplands; and their foraging habitat, which consists of upland washes and the lowlands of the historic LCR floodplain and its immediate vicinity. LCR MSCP management responsibilities lie within its planning area, in cooperation with other Federal agencies, States, and Tribes. This planning area encompasses only a few areas of upland. Management responsibilities for species conservation across the uplands surrounding the LCR MSCP planning area lie with these States, Tribes, and other Federal agencies, particularly the Bureau of Land Management and the U.S. Fish and Wildlife Service (USFWS).

This CEM rests on the most recent comprehensive species accounts and reviews of the literature for CLNB (AZGFD 2014; Brown 2013; LCR MSCP 2016; NatureServe 2019; O’Shea et al. 2018; Western Bat Working Group 2019), along with the findings of studies (Elliott et al. 2017; Tobin and Chambers 2017) that these five reviews mostly do not address, including the findings of field investigations in the Lower Colorado River Valley by and for the LCR MSCP over the past roughly 15 years (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Brown 2006, 2010, 2013, *in press*; 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; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010)).

This CEM also incorporates the expert knowledge of LCR MSCP biologists, the results of genetic studies of CLNB centered on the Lower Colorado River Valley (Hill 2011, 2016, 2019a), and information presented at the annual Colorado River Terrestrial and Riparian meetings in 2014–2017² (Broderick 2014; Brown 2015; Brown and Rainey 2016; Calvert 2014, 2015, 2016c, 2017; Mixan 2015, 2016, 2017; Mixan and Diamond 2014b; Rubin et al. 2014). Finally, the CEM incorporates information on bat ecology and conservation in general from numerous sources, including Bunkley et al. (2015), Mikula (2015), and Mikula et al. (2016), and information on rabies transmission and effects in CLNB from Stuchin et al. (2018). However, the purpose of the present 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 this chapter briefly summarizes the reproductive ecology of CLNB, describes more fully the purpose of the CEM, and introduces the underlying concepts and structure of the

² No annual Colorado River Terrestrial and Riparian meetings took place in 2018 and 2019 due to temporary closures of the Federal Government.

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CEM. Succeeding chapters present and explain the CEM for CLNB within the greater Lower Colorado River Valley and identify possible implications of this information for species and habitat management, monitoring, and research needs.

CALIFORNIA LEAF-NOSED BAT REPRODUCTIVE ECOLOGY

Except where noted, the information in this section of chapter 1 comes from the AZGFD (2014), Brown (2013), the LCR MSCP (2016), NatureServe (2019), O’Shea et al. (2018), and the Western Bat Working Group (2019).

CLNB is the most northerly of the New World leaf-nosed bats (Phyllostomidae), a family with more than 140 species that display “... the largest diversity of food habits among mammalian families, including frugivorous, nectarivorous, insectivorous, carnivorous and blood-eating species” (Cruz-Neto et al. 2001). CLNB is the only member of this mostly Neotropical family to live year round in the continental United States. Its current range consists of the Lower Sonoran Desert life zone in southeastern California, southern Nevada, and southwestern Arizona, United States, as well as in Baja California, Baja California Sur, and most of Sonora, northern Sinaloa, and western Chihuahua, Mexico. CLNB do not migrate within this overall range; most remain their whole lives in the vicinity of their natal site, although they shift seasonally between cold- and warm-season roosting sites, which may be located in different caves or mines or simply in different portions of the same cave or mine (see chapter 3, “Inter-Site Movement,” “Roosting: Cold-Season,” and “Roosting: Warm-Season”).

Brown (2013) states:

California leaf-nosed bats neither hibernate nor migrate and have a narrow thermal-neutral zone. They are incapable of lowering their body temperature to become torpid. No special physiological adaptations occur in California leaf-nosed bats for desert existence, and behavioral adaptations such as foraging methods and roost selection contribute to their successful exploitation of the temperate zone desert even during the cooler months (Bell et al. 1986). To remain active year long in the temperate zone deserts, California leaf-nosed bats use warm, diurnal roosts in caves, mines and buildings with temperatures that often exceed 27 degrees Celsius (°C).

However, this summary understates the extent of CLNB physiological adaptations. CLNB have evolved an ability to strongly concentrate urine, and thus conserve water, and they can survive on a diet of larger insects and even tree lizards (*Urosaurus ornatus*) (see chapter 3, “Foraging” and chapter 4, “Arthropod Community” and “Vertebrate Community”), from which they are able to obtain a

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significant fraction of their daily water needs. As a result, as noted by the AZGFD (2014), “Some individuals in captivity have been reported to go for at least 6 weeks without drinking water (Lu and Bleier 1981).”

CLNB, since its first identification in the second half of the nineteenth century, have been variously classified as a separate species, included in the species of the Waterhouse’s leaf-nosed bat (*M. waterhousii*) or classified as a subspecies of the latter (*M. w. californicus*). However, chromosomal, electrophoretic, and morphologic analyses published in the mid-1970s resolved the confusion in favor of distinguishing CLNB and Waterhouse’s leaf-nosed bats as distinct species. The latter has a more tropical distribution across southern and central Mexico and the Caribbean. The ranges of the two species overlap in central Mexico, but the two are not known to hybridize. Further, “The results of a renal (kidney) morphology study show that [California] leaf-nosed bats can use drier habitats than Waterhouse’s leaf-nosed bats because of their greater ability to concentrate urine and conserve water” (LCR MSCP 2016).

While genetically distinct from Waterhouse’s leaf-nosed bats, CLNB are genetically diverse relative to each other. Hill (2011, 2016, 2019a) analyzed data on 916 base pairs of the cytochrome b mitochondrial deoxyribonucleic acid (mtDNA) gene sequenced from 102 individuals from 17 geographic localities across the United States (including the Lower Colorado River Valley) and Mexico. The analysis identified 18 haplotypes, only 5 of which occurred in the Lower Colorado River Valley, including 3 that were unique to the valley. Nuclear deoxyribonucleic acid (DNA) microsatellite data analyzed in the same study showed greater genetic variation in samples from the southern portion of the sampled range but also less variation between sampled groups relative to the mitochondrial data.

CLNB fit 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 (Speakman 1991a, 1995; Rydell et al. 1996).” However, the literature provides little information on the details of this reproductive adaptation in CLNB. The reproductive anatomy and endocrinology of CLNB are well studied (Crichton and Krutzsch 2000), but its reproductive ecology is not.

The recent species accounts for CLNB on which this CEM rests (AZGFD 2014; Brown 2013; LCR MSCP 2016; NatureServe 2019; O’Shea et al. 2018; Western Bat Working Group 2019) all cite the same limited observations that individual CLNB lives can span up to 15 years in the wild. Bat species that hibernate generally have longer lives than those that do not (Wilkinson and South 2002), and CLNB do not hibernate. Brown (2013) specifically comments that “This [15-year lifespan] record for California leaf-nosed bats is remarkable because a

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long lifespan in bats is usually attributed in some part to their ability to undergo daily and seasonal torpor.” CLNB do not exhibit either daily or seasonal torpor (O’Shea et al. 2018).

More substantial data indicate that reproductive females rarely give birth to more than a single pup per year. Early records suggested that CLNB frequently give birth to twins, but subsequent investigations found the opposite (O’Shea et al. 2018). On the other hand, warm-season capture surveys of CLNB in maternity colonies and while foraging, in the greater Lower Colorado River Valley and elsewhere, often encounter both reproductive and non-reproductive females (Calvert 2012a, 2016a). O’Shea et al. (2018) state:

Some ... natural history observations on litter size suggest that natality is high, although all such observations stem from captures at maternity roosts. Huey (1925) reported all of 12 females taken at a maternity colony in a mine during May 1924 were pregnant. One study found that 95% of 188 females taken in mist nets over water in southern Arizona during the maternity season were reproductive, although the great majority of these were lactating and thus had greater water needs (Schmidt, 1999), perhaps adding a positive bias. Nonetheless, this result was identical to the simultaneous finding that 95% of 268 females taken at maternity roosts in the nearby Agua Dulce Mountains also were reproductive (Schmidt, 1999).

The presence of both reproductive and non-reproductive females at the same time indicates that some females forego reproduction in some years. This presumably results in an actual birth rate of less than one pup per female per year. However, O’Shea et al. (2018) report that they were unable to find any published literature with quantitative data on CLNB inter-birth intervals. The literature reviewed for this CEM also provides no information on factors that might affect the annual rate of female reproductive participation (see chapter 2, “Introduction to the California Leaf-nosed Bat Life Cycle” and chapter 3, “Breeding”).

Unlike many other bats of the United States, the CLNB adult female does not store the sperm it receives in autumn during mating and delay fertilization and implantation until spring. Rather, CLNB egg fertilization and implantation take place in autumn immediately after mating, with the female metabolically delaying most embryonic growth until spring. This results in a longer pregnancy compared to other bats of the United States, over the course of which more factors presumably could impinge on reproductive success. However, the literature reviewed for this CEM also provides no information on the rates or limiting factors for successful CLNB pregnancies.

Finally, none of the publications reviewed for this CEM provide estimates of CLNB embryo, pup, or adult mortality or survival rates. The literature does not indicate any specific reasons for this lack of estimates despite an abundance of tracking data (Brown 2013).

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CLNB exhibit several behaviors that may be adaptations to avoid or reduce predation:

- A pattern of avoiding foraging during nights illuminated strongly by moonlight, known as “lunar phobia,” is documented among some bats around the world and interpreted to be a result of selective pressure from nocturnal predatory birds (Lang et al. 2006; Mikula et al. 2016; Saldaña-Vázquez and Munguía-Rosas 2013). Investigations of bats along the Lower Colorado River Valley have found evidence for lunar phobia only among CLNB (Brown 2006, 2010, 2013, 2015; Vizcarra 2011; Vizcarra and Piest 2010; Vizcarra et al. 2010). CLNB tend to remain in their roosting sites in mines along the greater Lower Colorado River Valley during the brightest portions of the lunar cycle, resulting in depressed nocturnal exit numbers at mine openings during these times. Hill (2018) recommends that “The week before a full moon should be avoided if possible [for mist-netting along the Lower Colorado River Valley], as California leaf-nosed bats have been found to be lunar phobic.”
- Worldwide, roosting by bats in caves and cave analogs (e.g., mines) also is thought to result in lower rates of predation compared to roosting in trees (Wilkinson and South 2002).
- Investigators (e.g., as summarized by Brown 2013; O’Shea et al. 2018) consistently describe the flight of CLNB as extremely maneuverable, rapid, and silent, although they can also fly slowly and hover when targeting prey. Their echolocation calls are extremely quiet. Tuttle (1998) describes their echolocation calls as “... special whispering-type signals that can be heard no more than three feet away, preventing most prey from anticipating their approach until it is too late.” Further, CLNB appear to have unusually acute hearing and night vision (Tuttle 1998) and often hunt visually rather than through echolocation. While these characteristics necessarily benefit CLNB during foraging, it is plausible that they also allow CLNB to detect and avoid predators from the air and possibly from the ground as well, at least out in the open, where the bats have room to maneuver (versus within or at the confined openings to caves or underground mines).
- Ammonia from decomposing bat droppings in the enclosed spaces of caves and underground mines can rise to concentrations that are both noxious and toxic to many other mammals. However, CLNB have evolved physiologically to tolerate extremely high concentrations of ammonia in their day-roosting sites (see chapter 3, “Competition”). While noted as a mechanism that may reduce competition with CLNB from other bats for roosting space (Tuttle 1998), it is plausible that this adaptation also reduces daytime predation on CLNB as well.

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Conversely, CLNB foraging behaviors potentially could subject them to higher rates of predation. CLNB have been observed foraging within 1 meter (m) of the ground, often sometimes foraging close to vegetation, including gleaning prey directly off vegetation surfaces. Foraging CLNB therefore more often come within reach of ground-based predators compared to bats that forage higher above the ground or vegetation. Further, because they do not hibernate and remain active year round, including foraging for approximately 2 hours per night during the cold season, CLNB face pressure from predators outside protective cave or mine environments for a greater fraction of the year compared to bats that do hibernate.

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 (DiGennaro et al. 2012; Fischenich 2008). 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.

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

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- **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

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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 (HCP) (LCR MSCP 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 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.

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 as noted above. 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

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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, these CEMs focus 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.

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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

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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 (life stages, life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors) for each species, 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

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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 to 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 it may identify the critical biological activities or processes for a life stage with the greatest number of poorly understood drivers or effects.

Chapter 2 – California Leaf-nosed 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 CLNB in the Lower Colorado River Valley on which to build the CEM. Except where noted, the information in this chapter comes from the most recent comprehensive species accounts by the AZGFD (2014), Brown (2013), the LCR MSCP (2016), NatureServe (2019), O’Shea et al. (2018), and the Western Bat Working Group (2019). Table 1 and figure 1 summarize the proposed life stage model for CLNB in the Lower Colorado River Valley.

Table 1.—Proposed life stages and life-stage outcomes for the CLNB in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Pups	<ul style="list-style-type: none">• Pup growth• Pup survival
2. Adults	<ul style="list-style-type: none">• Adult growth• Adult survival• Adult fertility

INTRODUCTION TO THE CALIFORNIA LEAF-NOSED BAT LIFE CYCLE

The life cycle of CLNB, while similar to that of other cave-dwelling bats in North America, differs in at least two important ways.

First, as discussed in chapter 1, CLNB is the most northerly of New World leaf-nosed bats (Family Phyllostomidae) and the only member of this largely Neotropical family to live year round in the continental United States. At the same time, CLNB do not enter daily or seasonal cycles of torpor. Instead, CLNB have adapted to life outside the Neotropics by roosting only in warm regions and, within those regions, only in caves and mines with elevated internal temperatures. Further, and also unlike many other bats of the United States, the CLNB adult female does not store the sperm it receives in autumn during mating, delaying

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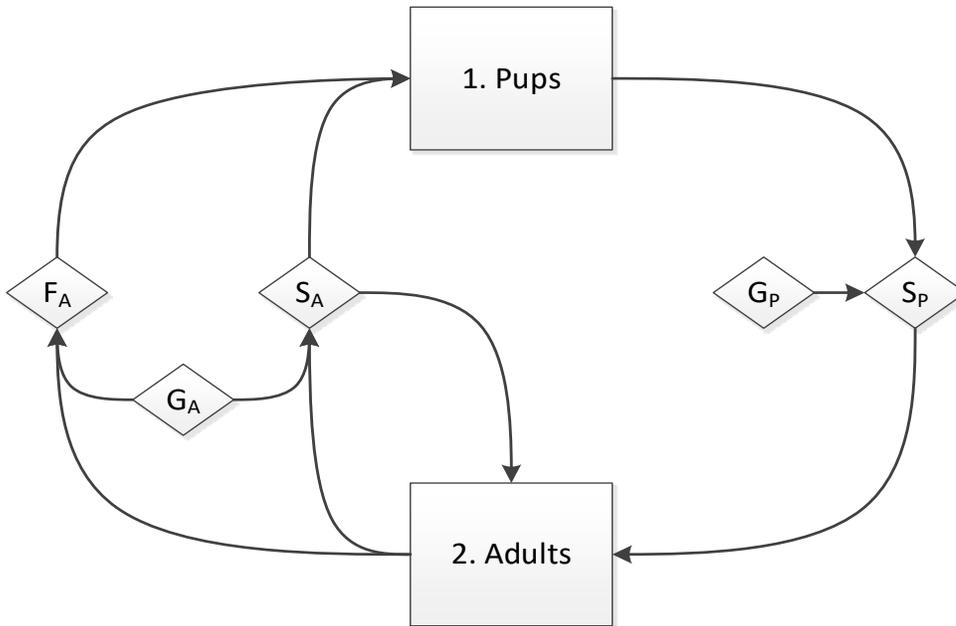


Figure 1.—Proposed life history model for the CLNB.

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.

fertilization and implantation until spring. Rather, fertilization and implantation of CLNB eggs takes place in autumn immediately after mating, with the female metabolically delaying most embryonic growth until spring.

Second, the literature on CLNB, both in general and for the Lower Colorado River Valley in particular, does not presently support distinguishing a “juvenile” life stage in the CEM separate from a preceding “pup” life stage or a subsequent “adult” life stage. The literature on other cave-dwelling bats in the greater LCR ecosystem, such as the Townsend’s big-eared bat (Braun and Unnasch 2020c), assign the label, juvenile, to individuals after they become volant and are weaned, until they become able to reproduce. During this intermediate life stage in other bat species, individuals experience additional bone growth, particularly epiphyseal-diaphyseal fusion in their wrists, as well as other changes leading to sexual maturation. Capture surveys—including in the Lower Colorado River Valley—typically use the state of wrist bone fusion visible with a headlamp to distinguish juveniles from adults (Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Hill 2018; Morgan et al. 2019). Among species for which age-specific survival data are available, such as Townsend’s big-eared bats (Braun and Unnasch 2020c), individuals in this intermediate life stage also have been found to experience a different (higher) rate of mortality than do individuals in the preceding or subsequent life stages.

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In contrast, the literature on CLNB presently does not distinguish a separate, intermediate life stage. As noted in chapter 1, the literature on CLNB presently also contains no survival data to assess for possible differences in mortality by life stage. Capture surveys of CLNB during their nocturnal foraging excursions at numerous sites along the Lower Colorado River Valley consistently observe lactating females, indicating an actively reproducing population (Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b). Roost surveys in caves along the valley similarly routinely observe non-volant pups (sometimes incidentally identified as “juveniles”), also indicating active reproduction (Brown 2010, 2013). However, the capture surveys nevertheless consistently fail to observe any juvenile CLNB based on wrist bone fusion (Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b). This combination of evidence suggests two possibilities:

1. Juvenile CLNB do not forage at the same times or in any of the same places as do CLNB adults, resulting in their not being detected in capture surveys targeted to capture foraging adults.
2. CLNB wrist bones fuse completely before or very shortly after they become volant, resulting in their wrists achieving adult conformation essentially simultaneously with volancy.

The first possibility seems unlikely: The literature contains no reports of investigations that have captured CLNB juveniles foraging separately from adults. In turn, while none of the literature reviewed for this CEM explicitly considers the second possibility, it nevertheless appears plausible. It is also consistent with observations of CLNB “juveniles” only in maternity colonies or being carried by lactating adults (Brown 2010, 2013). This CEM therefore does not recognize a separate CLNB juvenile life stage. Given present knowledge of CLNB biology and ecology, including a juvenile life stage in the CEM would not provide any additional information useful to species conservation. However, as knowledge expands, it may become useful to recognize a juvenile life stage in the CEM.

Including all volant CLNB in the adult life stage results in the inclusion of both sexually immature and mature individuals in this life stage. This CEM accommodates this circumstance by recognizing growth as a life-stage outcome for the adult life stage and breeding as a distinct, critical biological activity or process in which adults may engage depending on their state of growth, health, and other possible factors. This CEM also recognizes that adult female and male CLNB 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.

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The CEM recognizes a minimum of two life-stage outcomes for each of the two CLNB life stages—growth and survival. The CEM applies the term, growth, to both (1) morphological and physiological development and (2) the maintenance of body mass and condition (health) in the face of the stresses of daily life and fluctuations in outdoor air temperature and food availability. Pup growth includes morphological and physiological maintenance and development from birth to weaning. Adult growth includes morphological and physiological development from weaning to sexual maturity and the achievement of adult body mass; annual maintenance of body mass, including the building of fat stores to carry the individual through the cold season; and support of mating as well as subsequent gestation and lactation in females. Growth may be positive or negative and occur at different rates in females versus males. Survival for pups is the rate at which members of a local population survive through this 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 CLNB life history.

Pups

The pup life stage begins with the birth of the pup in a maternity colony, mostly from early May through early June (Brown 2010) but overall from mid-May to early July after a gestation period of almost 9 months. CLNB are born weighing approximately 25 to 30% their adult weight, which the literature variously states as 12 to 22 grams (AZGFD 2014) or 9.7 to 17.0 grams (O’Shea et al. 2018), averaging 11.7 grams (Cruz-Neto et al. 2001) or 12.75 grams (Arizona Sonora Desert Museum 2019). They are poikilothermic and depend on contact with their mothers, clustering of mothers within the maternity roost, and the location of the maternity roost—both the selection of the cave or mine itself and the selection of roosting location within the cave or mine—for thermal regulation. They nurse for approximately 1 month before becoming volant and beginning to forage for themselves. As discussed above (this chapter), mist-net captures of CLNB foraging along the Lower Colorado River Valley do not encounter individuals with immature skeletal development. This pattern suggests that CLNB pups reach adult size and skeletal maturity by the time they become volant, achieving a three- to fourfold increase in body mass during this life stage.

Adults

For the reasons stated above, this chapter, this CEM categorizes CLNB as adults when they reach adult size and skeletal maturity,. An unquantified but apparently

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large proportion of adult females breed in the first autumn following their birth, while all other females and all males become reproductively active only in their second year. As noted above (this chapter), a few adult females may forego reproduction in any given year. Records of non-reproductive males in warm-season captures of foraging CLNB (Calvert 2012a, 2016a) could indicate that males also physiologically are not be able to mate every year, although these records could merely represent males during their first year.

Adult CLNB follow a consistent pattern of seasonal activities and inter-site movements as follows:

- Males and females resume roosting together during the fall mating season after roosting separately in mostly female maternity colonies and mostly male bachelor colonies earlier in the warm season (see below, this chapter, and chapter 3, “Breeding,” “Inter-Site Movement,” and “Roosting: Interim”). The fall mating season begins in July – August but peaks in September – October. As summarized by Brown (2013):

“In early fall, males aggregate in display roosts and attempt to attract females with a courtship display consisting of wing flapping and vocalizations. Aggression between males occurs at this time. The areas used as ‘lek’ sites are usually in or near a mine that had been occupied by a maternity colony.”

Investigators in the Lower Colorado River Valley use the term, lek, in quotation marks because “While this behavior is similar to lekking observed in other species, the California leaf-nosed bat does not possess a true lek mating system” (Hill 2019a). Mixan et al. (2013; see also Mixan and Diamond 2014a) report increased acoustic detections of CLNB foraging along the Lower Colorado River Valley system-wide during the mating season.

- Males and females continue roosting together through the cold season in caves and underground mines with a distinct set of thermal and morphological characteristics (see chapter 3, “Roosting: Cold Season”). Cold-season roosting may occur in a different portion of the same cave or mine used during the mating season or in a separate but nearby cave or mine. Banding and genetic studies support an inference of strong fidelity (philopatry) to mating and cold-season location among CLNB, particularly females (Brown 2013; Hill 2019a). Females that have mated successfully begin gestating, but with a very slow rate of embryologic development that delays embryo maturation until the warm season. These cold-season colonies persist through winter. Neither females nor males hibernate, and they maintain their body temperature through their selection of roosting location—both their selection of the cave or mine itself and their selection

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of roosting location within the cave or mine—and by continuing to forage as well as burning stored body fat to sustain their metabolism. Tuttle (1998) notes:

“To survive winter, they must find the few available roosts that are geothermally heated; only mines or caves of approximately 84 °F will do. The bats emerge to feed in the cold for up to two hours at a time, even when temperatures fall to 50 °F, though they often cannot take in as much energy as they need. In February, they typically are able to find only about half of the food needed to maintain constant body weight, forcing them to rely on stored fat for the remainder.”

- CLNB embryo development begins to accelerate in March and April, at which time females and males begin shifting their roosting locations to maternity and bachelor colonies, respectively. Bachelor and maternity colonies may be located in different parts of the same cave or mine or in different caves or mines. The female-male separation at this time is not absolute: Maternity colonies may contain a few males (see below), and bachelor colonies may contain non-reproductive females. As summarized by Brown (2013):

“Females congregate in large (> 100 bats) maternity colonies in spring and summer, utilizing different mines or areas within a mine separate from those occupied in winter, although colonies of only 6–20 bats are also found ... Mine complexes often provide both summer and winter roosting areas, with the females moving closer to the entrance in the maternity season. The males may continue to roost in the deeper sections of the mine. Multiple-entrance mines are a common feature for most maternity colonies; the entrances create cross-ventilation, which may make the roosts warmer during the day, a factor that could facilitate development of young bats.

Within the larger maternity colonies, clusters of 5 to 25 females will be associated with a single “harem” male that defends the cluster against intruding males (Berry and Brown 1995). The discovery of possible “harem” formation within the maternity colony has several interesting interpretations (Brown and Berry 1991). Males are observed “wing flapping” and vocalizing in the presence of pregnant females and those with young babies at a time when viable sperm are not present. The males appear to drive away other males that enter their sphere of influence. Although some male wing flapping is observed at all times of the year, this behavior is most pronounced when females have babies. Possible explanations are that the male has sired the young and is protecting them or that the females are “imprinting” on the male for future breeding purposes. Large male-only roosts may also form in spring and summer, such as at the Hart Mine.”

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- Females give birth to a (usually) single pup mostly in June (overall mid-May to early July). Mothers nurse (and presumably also groom) their pups and regulate pup temperature through bodily contact, clustering with other mothers within the maternity roost, and selecting suitable roosting locations (see above, this chapter). As noted above (this chapter), they nurse for approximately 1 month before the pups become volant and begin foraging for themselves. Maternity colonies disband once the young are independent in late summer. Females and males then begin regathering for mating. The literature reviewed for this CEM does not discuss the roosting patterns of either males or females prior to their coming together again in the mating season.

CLNB adults forage daily over the course of this annual cycle of activity, including during the cold season, as noted above. Their foraging behaviors include the use of night roosts within or close to their foraging habitat, where they consume prey too large to consume mid-flight. Potential night-roosting locations for CLNB include cavities in high cliffs and the banks of deep washes, the interiors of unoccupied buildings, undersides of bridges, and cave-like cavities in stacks of hay bales (Maturango Museum and Brown-Berry Biological Consulting 2018). Foraging females with dependent pups may return to their maternity roosts several times nightly to care for their pups instead of using separate night roosts closer to their foraging areas (Maturango Museum and Brown-Berry Biological Consulting 2018). Further, "... most California leaf-nosed bats became inactive by midnight, and either night roosted near the foraging area or returned to the mine roost ... Bat activity typically increases in the hour before dawn, and the bats may forage again before returning to their day roosts" (Maturango Museum and Brown-Berry Biological Consulting 2018). This temporal pattern of foraging holds at all times except during periods of greatest moonlight. As noted in chapter 1, CLNB exhibit lunar phobia and exit their daytime roosting sites in much lower numbers when the moon is full (or nearly so) than during other parts of the lunar cycle.

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 15 critical biological activities and processes that affect 1 or both CLNB 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 15 critical biological activities and processes and their distribution across life stages.

Table 2.—Proposed critical biological activities and processes for the CLBN 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	Adults
Breeding		X
Chemical stress	X	X
Competition		X
Disease	X	X
Drinking		X
Feeding	X	
Foraging		X
Inter-site movement		X
Maternal care		X
Mechanical stress	X	X
Predation	X	X
Roosting: cold season		X
Roosting: warm season	X	X
Roosting: interim		X
Thermal stress	X	X

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BREEDING

This critical biological activity or process consists of a suite of more specific biological activities and processes, including mating aggregation and display, mate selection, mating (copulation), egg fertilization and implantation, possible “harem” behaviors, gestation, and birthing, as described in chapter 2. The suite of more specific biological activities and processes included here under the umbrella term, breeding, does not include maternal care, which the CEM addresses as a separate critical biological activity or process. The suite of more specific biological activities and processes included under the umbrella term, breeding, may or may not include abortion or resorption of embryos or abandonment of dependent pups as a result of stress. Terminations of the breeding cycle in this way are known to occur among Townsend’s big-eared bats as consequences of drought or poor foraging during the gestation period or anthropogenic disturbances to maternity colonies (Braun and Unnasch 2020c). However, the literature reviewed for this CEM does not mention evidence of any types of terminations in CLNB.

Chapter 2 summarizes the CLNB annual breeding cycle, including lekking-like and harem-like behaviors. The rates of all steps in the breeding cycle may or are known to vary. However, the ranges of variation in these rates among CLNB are mostly not known. The factors shaping this variation similarly are not known.

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 (1) the organism can detect these conditions and (2) the conditions are sufficiently localized to permit such avoidance or escape.

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Chemical stress is recognized or suspected as a threat across all bat species in North America (Crichton and Krutzsch 2000; Hammerson et al. 2017; Hernández-Jerez et al. 2019; Tuttle and Moreno 2005; Voigt and Kingston 2016). The literature therefore also proposes that chemical stress is a threat to CLNB in particular (Brown 2006; NatureServe 2019). Potential sources of exposure for CLNB in the Lower Colorado River Valley could include agricultural pesticides and herbicides and industrial contaminants in and around abandoned underground mines (see chapter 4, “Chemical Contaminants”). O’Shea et al. (2018) report:

King et al. (2001) reported on concentrations of potentially toxic elements and organochlorines in small numbers of bats sampled at two sites in Arizona (four samples for organochlorines) and California (five samples analyzed for organochlorines, six for metals) in 1998. None of the bats had concentrations of toxic elements indicative of harmful effects, and organochlorines were present only at very low concentrations. However, King et al. (2003) analyzed a larger sample of individuals at former mine sites on the Kofa National Wildlife Refuge [northeast of Yuma, Arizona, between the LCR and Gila River valleys] in 2001 and 2002, including two abandoned lead mines. They reported lead in carcasses and livers of these bats from the former lead mines at exceptionally high concentrations but were unable to directly link these high concentrations with impacts on the health of the bats. King et al. (2003) also found very high lead levels in the soils from the floor of these mines and hypothesized that the leaf-nosed bats were accumulating lead through grooming lead particles from dust on the fur and from inhaling lead-contaminated dust within the mines. The analyses in this study also included up to 17 other toxic elements, but concentrations of these other elements were not considered to be elevated.

The literature reviewed for this CEM otherwise does not include evidence of chemical stress among CLNB or otherwise directly address the topic.

This CEM categorizes hydration stress as a form of chemical stress (see also chapter 4, “Water Availability”). CLNB appear to have evolved specific physiological adaptations to living in a hot, arid environment that allows them to make the most of scarce water resources as discussed in chapter 1.

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.

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As noted in chapter 1, adult male CLNB may compete to attract females for copulation, in lekking-like behavior, and may guard females in harem-like behavior. CLNB females do not store sperm from mates for delayed fertilization, an adaptation thought to facilitate sperm competition in other bat species (Orr and Zuk 2013). CLNB pups do not compete with each other for maternal care because CLNB females only rarely give birth to more than a single pup per year.

The evidence is ambiguous for whether CLNB adults 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).

CLNB do not roost in the direct company of members of other bat species. However, it is not uncommon for colonies of several bat species to occupy different locations within the same cave or abandoned underground mine. Bat roost surveys at 12 abandoned underground mines in the greater Lower Colorado River Valley from 2002 to 2016 (Brown, *in press*) found the following co-occurrences:

- CLNB occurred in all 12 mines.
- Yuma myotis (*Myotis yumanensis*) occurred in 10 mines.
- Cave myotis (*Myotis velifer*) occurred 7 mines.
- Townsend's big-eared bats occurred in 4 mines.
- Pallid bats (*Antrozous pallidus*), California myotis (*Myotis californicus*), Mexican free-tailed bats (*Tadarida brasiliensis*), and big brown bats (*Eptesicus fuscus*) occurred in 3 mines each.
- Canyon bats (formerly western pipistrelle) (*Perimyotis hesperus*) occurred in 2 mines.

Nevertheless, as summarized by J. Hill (2020, personal communication), "CLNB generally occupy the parts of the cave closer to the entrance both for thermoregulatory purposes and presumably in response to the presence of other bat species."

Tuttle (1998) provides additional hypotheses on the ways in which CLNB have evolved to reduce competition with other bat species as follows:

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*Occasionally, these bats share roosts with other species, such as the Mexican free-tailed bat (*Tadarida brasiliensis*). Conditions in free-tail caves are far from ideal, however. The ammonia levels—caused by gas emanating from dermestid beetles feeding upon bat droppings—can be life-threatening to other animals. To survive, California leaf-nosed bats reduce their respiratory and cardiac rates by as much as 60 percent. With this change, carbon dioxide is retained in the blood and in respiratory mucus, buffering the ammonia's toxic effects. An ammonia level of 250 parts per million can be highly hazardous to humans within an hour or two. The bats can tolerate up to 3,000 parts per million for as long as nine hours. Competition for food with free-tails and other roost mates is rarely a problem because of the California leaf-nosed bat's unique feeding strategy and food choices. Free-tailed bats fly high in the sky, like little jets, often feeding on flocks of migratory moths, while leaf-nosed bats search slowly, close to the ground, for insects perched in plant foliage. They prefer rather large insects—approximately 1½ to 2 inches long (40 to 60 mm)—but will target prey as small as pill bugs (*Isopoda*). More common foods include a variety of grasshoppers and katydids; June beetles and diving beetles; and sphinx, underwing, and noctuid moths. These bats are the only ones in North America known to catch caterpillars and are among the very few insect-eating bats that supplement their diets with cactus fruit.*

As discussed below, this chapter (see “Foraging”) and in chapter 4 (see “Vertebrate Community”), CLNB in the Lower Colorado River Valley also eat tree lizards. This dietary behavior is not reported among the other bats of the valley (Brown 2013), and therefore presents an additional example of resource partitioning among bat species. On the other hand, many other species may prey on the same food items consumed by CLNB.

DISEASE

Disease consists of physiological and even anatomical disruptions to an organism as a result of their exposure to one or more pathogens. CLNB presumably are susceptible to a range of pathogens, including parasites (see chapter 4, “Infectious Agents”). Lethal infections result in mortality. Non-lethal infections may make affected individuals vulnerable to mortality from other causes, and other types of stress correspondingly may increase susceptibility to disease. Unfortunately, there are no data on CLNB survival rates, let alone analyses that attempt to break down these figures by potential cause. Further, it is generally considered difficult to separate causes of mortality among bats (Messenger et al. 2003).

CLNB can host the rabies virus, and infections can be fatal (Constantine 1979; Stuchin et al. 2018). The literature reviewed for this CEM otherwise provides no information on bacterial, viral, fungal, or parasitic disease among CLNB, indicating a large gap in knowledge (see chapter 4, “Infectious Agents”).

DRINKING

This CEM includes “drinking” as a critical biological activity or process, whereas the CEMs prepared to date for other bat species of concern to the LCR MSCP—the western red bat, western yellow bat, and Townsend’s big-eared bat (Braun and Unnasch 2020a, 2020b, 2020c)—do not. Distinguishing drinking as a critical biological activity or process is warranted for CLNB because their drinking behavior appears to affect their foraging behavior (see below, this chapter, “Foraging”) and reduces the effectiveness of different methods for their monitoring and capture (see chapter 4, “Monitoring, Capture, Handling”). CLNB drinking behavior thus has implications for species conservation. Drinking adaptations do not appear to have such ramifications for the other three aforementioned bat species.

CLNB appear to have evolved specific physiological adaptations to living in a hot, arid environment that allow them to make the most of scarce water resources as discussed in chapter 1 and above, this chapter (see “Chemical Stress”). These adaptations include being able to strongly concentrate urine, and thus conserve water, and a diet of larger insects and even tree lizards from which they are able to obtain a significant fraction of their daily water needs (see chapter 3, “Foraging” and chapter 4, “Arthropod Community” and “Vertebrate Community”). As a result, as noted by the AZGFD (2014), “Some individuals in captivity have been reported to go for at least 6 weeks without drinking water (Lu and Bleier 1981).”

Tuttle (1998) goes so far as to assert, “Although they [CLNB] live in some of North America’s most extreme deserts, they have never been seen drinking.” This exaggerates, but not by much: CLNB adults do occasionally drink from surface water sources. As noted by Brown and co-authors (Brown 2010, 2013; Brown *in press*):

*Open water for drinking does not appear to be a criterion for roost selection since some roosts are located over 50 km (31 miles) away from the nearest known water source. The bats exist primarily on moisture contained in the juicy insects that they consume (Bell et al., 1986). Radio telemetry studies designed to determine foraging habitat of *Macrotus* in the California and Arizona deserts indicated that the bats did not visit areas of open water (Brown et al., 1993; Brown et al., 1999; Dalton et al., 2000). Schmidt (1999) did mist net *Macrotus* (especially lactating females) over water sources in the southern Arizona desert. *Macrotus* are regularly netted at a pool along the Bill Williams River (Brown and Berry, 2003).*

Rabe and Rosenstock (2005) regularly caught CLNB in mist nets over natural and artificially modified tinajas in a study area across Kofa National Wildlife Refuge and the U.S. Army–Yuma Proving Ground in southwestern Arizona, an upland setting. However, they did not catch any CLNB over any of the

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smaller artificial watering features they monitored, including concrete-lined troughs and vaults. CLNB also can hover (O’Shea et al. 2018), potentially allowing them to drink from smaller pools than may be the case with bats that hover less.

None of the literature reviewed for this CEM provides observations of CLNB drinking behavior. This CEM assumes that this behavior resembles that of other bats species, consisting of gliding over the water surface and dipping briefly to the water surface. Such behavior brings bats close to potential aquatic predators such as fish and amphibians (Mikula 2015). On the other hand, the abilities of CLNB to obtain most of their moisture from their food and to conserve water from their urine both reduce this vulnerability. These abilities also could affect their monitoring by reducing the time they spend over water compared to time spent by other bats (Rabe and Rosenstock 2005) (see chapter 4, “Water Availability”).

FEEDING

CLNB pups obtain all of their food passively from their mothers, in contrast to CLNB adults, which actively forage for their food. The pup life stage in fact ends when the pup becomes able to forage for itself. 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 “Competition”), CLNB pups usually are born singly and do not need to compete for food with siblings in the same litter.

FORAGING

Foraging includes both the efforts taken to locate, capture, and consume prey and the efforts taken to commute between roosting and foraging sites. Investigations and reporting on CLNB diet and foraging behaviors span more than a century. As a result, this is perhaps the best known aspect of CLNB ecology. All of the recent comprehensive species accounts for CLNB (AZGFD 2014; Brown 2013; LCR MSCP 2016; NatureServe 2019; O’Shea et al. 2018; Western Bat Working Group 2019) provide summaries of this area of knowledge. The summary by O’Shea et al. (2018) is the most comprehensive, covering diet, flight characteristics during foraging, travel distances between day roosts and foraging areas, and the use of night roosts. Rather than paraphrasing, this summary is best quoted in full:

These bats forage in desert habitats and seem to favor desert washes, at least during the warmer months, where they glean insects from riparian vegetation and the ground (Brown and Berry, 1991; Schmidt, 1999). Taking prey from the ground was first suggested by Hilda Grinnell (1914) who noted the capture of a

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California leaf-nosed bat in a mouse trap in 1908 and speculated that it was attracted to insects feeding on the bait. Banding and radio-tracking studies in the Cargo Muchacho Mountains of southeastern California have shown that in the area studied, these bats rarely travel more than five to ten kilometers from their roosts and forage primarily in desert washes where they were observed feeding on large moths and katydids (Brown et al., 1993a,b).

Vaughan (1959) described the flight of these bats as extremely maneuverable and rapid, but noted that while foraging their flight can be slow, buoyant, nearly silent, and will include hovering. Individuals watched while foraging flew within one meter of the ground, often dropping closer, and also foraged close to vegetation (Vaughan, 1959). Stomach contents of these bats taken in the Riverside Mountains of California included many forms that were taken on the ground or from the surfaces of vegetation, including orthopterans (grasshoppers and crickets), noctuid moths and caterpillars, and scarab and carabid beetles (Vaughan, 1959); they will also alight on ceilings of grottos, caves, and abandoned mines to manipulate and consume larger prey items such as sphinx moths, grasshoppers, and beetles (Huey, 1925; Vaughan, 1959; Ross, 1964).

*Ross (1964, 1967) examined 41 digestive tracts from individuals taken in both Arizona and in Mexico. Typical insect prey sizes ranged 40 to 60 millimeters and the bats primarily consumed the abdomens of the larger prey items. However, smaller items ranging down to 20 millimeters were also noted, including flying ants. As in California, prey included large slow-flying insects and mainly terrestrial species such as sphinx moths, short-horned and long-horned grasshoppers (*Acrididae* and *Tettigoniidae*), long-horned beetles (*Cerambycidae*), and caterpillars. Ross (1964) also reported that stomachs of these bats contained fruit or other vegetative matter, but these specimens were likely *M. waterhousii* taken in Mexico prior to a revised understanding of the systematics of *Macrotus*. Food items summarized from the literature by Bradshaw (1961) included coleopterans (*Carabidae*, *Meloidae*, and *Scarabaeidae*), orthopterans (including grasshoppers), lepidopterans (*Sphingidae*, *Noctuidae*, *Cossidae*, and caterpillars), odonates (dragonflies), homopterans (cicadas), dipterans, and hymenopterans. Other reports of prey include cockroaches and diurnal acridid grasshoppers and nymphalid butterflies (Bell et al., 1986), as well as small lizards (Brown, 2013). Many of these prey items were probably taken from the ground or surfaces of vegetation (Vaughan, 1959; Bradshaw, 1961; Bell, 1985).*

California leaf-nosed bats have echolocation characteristics that are well suited for foraging in the cluttered situations encountered by species that glean prey from vegetation and ground surfaces (low intensity, high frequency, and short duration ultrasonic pulses), particularly in total darkness; they will also cue on audible sounds made by prey (Bell 1985). However, vision is very well developed compared to many other insectivorous bats, and they regularly interrupt echolocation and switch to vision to locate insects, particularly under moonlight conditions (Bell, 1985; Bell and Fenton, 1986).

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Anderson (1969) also states the following concerning CLNB foraging:

Flight is highly maneuverable, may be rapid but during foraging is usually slow and relatively silent, within a meter of the ground and often close to vegetation. They often hover, alight by an upward swoop and half-roll, launch by dropping a short distance before taking wing or by flying directly from the roost, and may ingest prey after alighting. They emerge 30 minutes or more after sunset, usually about 90 to 120 minutes after, temporary night roosts may be different from day roosts. There are two main feeding periods, the second about the hour 01:00, and each bat probably is on the wing less than 105 minutes each night.

Other publications, particularly for the greater Lower Colorado River Valley, provide additional information on CLNB foraging or, for one topic, provide an alternative perspective, as follows:

- CLNB may occasionally capture and consume tree lizards. Specifically, Brown (2010) reports:

*During the current project, we discovered a *Macrotus* in a night roost at Jackpot #3 [in Havasu National Wildlife Refuge] chewing on the head of a wiggling tree lizard... This reptile spends most of its time in trees and scrubs, often clinging head downward (Stebbins, 1985). The *Macrotus* probably gleaned it from the branches of a desert tree when the lizard was sleeping. Since then, we have observed with night vision equipment as *Macrotus* carry lizards back into the mines after dark. The intestinal tract appears to be all that remains after the bat consumes the lizard.*

- Ross (1964) cites personal communications of observations of CLNB in Baja California, Mexico, feeding on fruit of the organpipe cactus (*Stenocereus thurberi*; formerly *Lemaireocereus thurberi*), which does not occur along the Lower Colorado River Valley. While O'Shea et al. (2018) question this evidence for CLNB consumption of fruit and other vegetal matter, the Arizona-Sonora Desert Museum (2019), the AZGFD (2014), the LCR MSCP (2016), NatureServe (2019), and Tuttle (1998) find the evidence convincing. Fruit consumption would be an additional example of foraging by gleaning directly off vegetation. However, vegetal matter in CLNB stomachs also could come from the guts of large herbivorous arthropods, such as grasshoppers, on which CLNB feed. Huey (1925), examining fecal matter beneath a large colony of CLNB in an unnamed mine north of Potholes, Imperial County, California, specifically observed vegetal matter in. "... the gorged viscera of some large insect, perhaps those of grasshoppers," dissection of which "... found them tightly packed with vegetable matter."

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- As noted in chapter 1, female CLNB with dependent pups will return to the maternity colony several times during the night rather than use night roosts closer to or within their targeted foraging habitat.
- CLNB in the greater LCR ecosystem forage much more widely than simply in desert washes (see chapter 4, “Tree and Shrub Vegetation”). In fact, O’Shea et al. (2018) elsewhere state:

Natural history observations in California suggest that these bats utilize lower elevation desert habitats near preferred roosting sites in caves and abandoned mines, with foraging concentrated in desert washes and surrounding areas or over the river floodplain (Vaughan, 1959; Brown and Berry, 1991; Brown et al., 1993a, b)... Differential use of habitat types within riparian areas in the Mojave Desert of southern Nevada by these bats was studied primarily using acoustic detections: California leaf-nosed bats occurred in each of four habitats (riparian marsh, mesquite bosque, riparian woodland, and riparian shrubland) about equally (Williams et al., 2006).

Acoustic and capture (mist-net) surveys along the LCR and Bill Williams River floodplains since 2002 consistently detect CLNB foraging in areas of bottomland tree and shrub vegetation, including areas dominated by Fremont cottonwood (*Populus fremontii*) and Goodding’s willow (*Salix gooddingii*), honey mesquite (*Prosopis glandulosa*), screwbean mesquite (*P. pubescens*), saltcedar (*Tamarix* spp.), marsh (primarily southern cattail, *Typha domingensis*, and California bulrush (*Schoenoplectus californicus*), and remnant native vegetation at the margins of irrigated agricultural fields (Berry et al. 2017; Broderick 2010, 2012a, 2012b, 2013, 2016; Calvert 2009, 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Diamond 2012; Diamond et al. 2013; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2012, 2013; Vizcarra 2011; Vizcarra and Piest 2009, 2010; Vizcarra et al. 2010). This includes foraging in LCR MSCP conservation areas and other habitat creation areas consisting of planted stands of cottonwood and willow.

- The findings from the aforementioned mist-net surveys complement those from contemporaneous radio telemetry studies along the greater Lower Colorado River Valley by Brown and colleagues (Brown 2010, 2013, 2015, *in press*; Brown and Rainey 2016; Maturango Museum and Brown-Berry Biological Consulting 2018). These telemetry studies tracked CLNB captured in both the cold and warm seasons, both in mines and in mist nets deployed within the LCR MSCP planning area, and subsequently tracked as they moved back and forth between foraging areas and day-roosting sites. The tracking efforts routinely detected CLNB moving downhill at night from their roosts in the mines to spread out and forage both along washes descending from the uplands and across the floodplain.

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- The radio telemetry of CLNB captured along the Lower Colorado River Valley floor (see above) found that they do not forage radially in all directions from their day-roosting sites; instead, their roosting sites more typically mark “the apex of a triangular fan directed toward the LCR” (Maturango Museum and Brown-Berry Biological Consulting 2018). Further, the radio-tracked CLNB were observed traveling more than 16 km (10 miles) in each direction between their roost and their most distant foraging area. Maturango Museum and Brown-Berry Biological Consulting (2018) note that, “This result has conservation implications since impact mitigation for some projects on public lands have required that foraging habitat be protected only within a 5-mile (8 km) radius of roost.” Vizcarra (2011) and Vizcarra et al. (2010) measured CLNB foraging activity along the Lower Colorado River Valley using data on call minutes detected during acoustic monitoring. CLNB foraging activity in this study statistically varied negatively with distance from day-roosting sites and distance from the river, and it did not vary statistically with the dominant vegetation type around fixed acoustic monitoring stations.
- The radio telemetry of CLNB captured along the Lower Colorado River Valley floor (see above) found that the bats had smaller foraging areas in winter and remained on the surface for shorter periods of time than in summer (Maturango Museum and Brown-Berry Biological Consulting 2018). Female CLNB were sometimes also found to travel slightly farther to forage, have larger overall foraging areas, and use different foraging areas compared to males (Maturango Museum and Brown-Berry Biological Consulting 2018). The radio telemetry of CLNB captured along the Lower Colorado River Valley floor (see above) also found that some individuals repeatedly returned to forage in the specific localities where they were first captured (Maturango Museum and Brown-Berry Biological Consulting 2018).

Finally, Brown (*in press*) notes that, “The [CLNB] strategy of gleaning larger prey from the substrate as compared to aerial insectivory appears to reduce the total time and energy necessary for foraging.”

INTER-SITE MOVEMENT

CLNB do not migrate and, as noted by Tuttle (1998), “Their short, broad wings and helicopter-like flight are not suited to long-distance travel.” Nevertheless, CLNB exhibit four kinds of inter-site movement, as summarized in chapter 2. This critical biological activity or process concerns movements between sites where the bats roost for one or more consecutive days and does not concern movements between such sites and night feeding sites during foraging excursions (see above, this chapter, “Foraging”).

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The four kinds of inter-site movement among CLNB are: (1) movement from their cold-season roosting sites to warm-season roosting sites, the latter being either maternity sites, mostly occupied by reproductive females, or bachelor sites, occupied by males and non-reproductive females, (2) movement from their warm-season roosting sites to aggregate at display roosts for mating, (3) movement from their display roosts to cold-season roosting sites, and (4) movement from one cold-season or warm-season roosting site to another.

Investigators have banded over 25,000 CLNB along the LCR from Parker Dam to Yuma since 1964 to assess longevity and movement patterns, the latter by comparing the sites of banding to the sites of recapture (Brown 2013). Most of these banding and recapture efforts took place in winter. This long-term study followed a banding study covering all months of the year from July 1959 to March 1964 across Mohave County, Arizona, that banded nearly 2,100 CLNB (Cockrum et al. 1996). In combination, these two banding studies indicate the following (Brown 2013; O’Shea et al. 2018):

- In the Mohave County study, the greatest distance between a cold-season roost to a maternity colony documented was 93 km, and the greatest linear distance between banding and recapture sites of any kind was 137 km. For the investigations along the Lower Colorado River Valley, Brown (2013) reports:

The longest distance between the site of banding and that of recapture was a movement over two mountain ranges for a linear distance of 87 km. Most banded California leaf-nosed bats traveled only a few kilometers between summer and winter roosts (Brown and Berry 1998). However, bats recently banded in winter at the Californian Mine have been recaptured in mist nets in summer near Planet Ranch [approximately 19 km distant] along the Bill Williams River (Calvert 2012a, personal communication).

- Both studies recaptured the majority of CLNB within a few kilometers of the roosting site where they were banded. Brown (2013) reports for the longer-term study that “... many of these bats were recaptured up to 10 times with an average 50-percent recapture success rate, suggesting strong roost fidelity.”
- The genetic studies by Hill (2011, 2016, 2019a) similarly indicate that CLNB sustain some genetic differences between localities, consistent with a limited extent of dispersal between localities. Nevertheless, CLNB do disperse sufficiently between localities to sustain at least some genetic mixing throughout the overall species range. The nuclear DNA findings by Hill (2019a) support an inference of greater dispersal by males than by females (i.e., a higher degree of philopatry among females than males) (J. Hill 2020, personal communication).

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At the same time, the literature reviewed for this CEM does not address, or addresses only anecdotally, several details of CLNB inter-site movement that potentially could have implications for species or habitat management. Specifically, the literature does not indicate whether CLNB use temporary day roosts during their longer-distance travels between seasonal roosting sites. The literature reviewed here also does not indicate how readily, how often, or why CLNB may move from one cold- or warm-season roosting site to another other than to note that such relocations can occur and, at least for cold-season relocations, can occur in response to disturbances (O’Shea et al. 2018). Finally, the literature reviewed for this CEM does not indicate what factors might influence whether and how far CLNB may move away from the vicinity of their natal (maternity) roost over the course of their lifetime.

MATERNAL CARE

CLNB 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”).

Maternal care of pups in maternity colonies includes feeding (nursing), and eventually weaning the pups, and providing a safe thermal environment. As noted in chapters 1 and 2, CLNB pups are poikilothermic and depend on contact with their mothers, clustering of mothers within the maternity roost, and the location of the maternity roost—both the selection of the cave or mine itself and the selection of roosting location within the cave or mine—for thermal regulation. Bats generally groom themselves using one foot while holding on with the other (Brown 2006, 2010); presumably maternal care also includes grooming of pups. However, the literature reviewed for this CEM does not address grooming of pups in CLNB.

As discussed above, this chapter (see “Breeding”), some cave-dwelling bats in North America, such as Townsend’s big-eared bats, are known to abandon their pups and their maternity roosting sites altogether following anthropogenic disturbance (Braun and Unnasch 2020c). However, the literature reviewed for this CEM does not mention evidence of such behavior in CLNB.

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. Unfortunately, there are no data on

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CLNB survival rates, let alone analyses that attempt to break down these figures by potential cause. Further, 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 CLNB adults, while recognizing that the subject remains unstudied in the Lower Colorado River Valley or elsewhere, and recognizing that the incidence of injury but not mortality from predation is rarely addressed for bats at all.

CLNB pups presumably may be injured if they fall from their roost, experience an unsuccessful attack by a predator, or are disturbed or handled by people. Adult CLNB 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”). For example, Maturango Museum and Brown-Berry Biological Consulting (2018) report that pregnant and lactating CLNB were found to be especially susceptible to injury and mortality from the attachment of radio transmitters: “A prior California leaf-nosed bat telemetry study resulted in the death of the both the lactating female and her pup (Brown et al. 1993). Consequently, bats have not been tracked during this reproductive period again” (see chapter 4, “Monitoring, Capture, Handling”). 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.

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.” O’Shea et al. (2018) also note, “This species may be more susceptible to accidental mortality (such as ensnarement on spines of desert plants; Stager, 1943a) than other species of bats because of their habit of foraging close to the ground.”

PREDATION

CLNB presumably face the potential for injury and mortality due to predation throughout their lives, as do all wild animals. Every animal species has evolved characteristics that permit its persistence despite predation, including specific behaviors, body features, and/or reproductive strategies that allow it to avoid,

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escape, deter, or counterbalance losses from predation. Unfortunately, there are no data on CLNB survival rates, let alone analyses that attempt to break down these figures by potential cause. Further, 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 CLNB adults, while recognizing that the subject remains unstudied in the Lower Colorado River Valley or elsewhere, and recognizing that the incidence of injury, but not mortality, from predation is rarely addressed for bats at all.

As noted in chapter 1, CLNB have evolved several characteristics that may help them avoid or limit their vulnerability to predation. These characteristics include the use of caves and cave analogs as day roosts; reduced foraging activity during brightly moon-lit nights (lunar phobia); extremely maneuverable, rapid, and silent flight; unusually acute hearing and night vision; and an ability to tolerate the presence of ammonia in their day-roosting sites at concentrations noxious and toxic to other mammals.

On the other hand, as also noted in chapter 1, CLNB may expose themselves to higher levels of risk from predation through their tendency to forage within 1 m of the ground and/or close to vegetation, including gleaning prey directly off vegetation surfaces. Further, because they do not hibernate and remain active year round, CLNB are exposed to predators outside protective cave or mine environments for a greater fraction of the year compared to bats that do hibernate.

CLNB also usually have only one pup per litter. A local population therefore cannot recover quickly from the effects of intense predation. On the other hand, CLNB may live up to approximately 15 years in the wild, and females may reproduce in their first year, allowing them to recover at least slowly from periods of intense predation.

Predators may attack CLNB in four settings: (1) in their day and night 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 or vegetation canopy, when their foraging activities bring them close to the ground or canopy. Further, because CLNB 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 CLNB in each of the four settings. Chapter 4 (see “Arthropod Community” and “Vertebrate Community”) identifies individual species and types of species that potentially could prey on CLNB in these settings.

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CLNB appear to locate their cold- and warm-season roosts within caves and underground mines solely on the basis of temperature (see below, this chapter, “Roosting” and “Thermal Stress;” and chapter 4, “Caves and Cave Analogs” and “Temperature”). As a result, they may roost in only semidarkness within only 8 to 23 m (25 to 75 feet) of the cave or mine entrance. Many carnivorous climbing mammals and climbing reptiles may be able to reach and forage in such settings. 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 CLNB 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.” The LCR MSCP (2016) specifically mentions an unpublished report of an individual CLNB “... found impaled on a barbed wire fence outside of a mine entrance near the Bill Williams River, likely by a loggerhead shrike (*Lanus ludovicianus*), which was found flying away from the mine entrance as people approached.”

Avian predators are likely the main threat to CLNB 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 CLNB at ground level (see chapter 4, “Vertebrate Community”). Additionally, Mikula (2015) suggests that, worldwide, fish and amphibians potentially can prey on bats at ground level when they come down at night to drink.

ROOSTING: COLD SEASON, WARM SEASON, INTERIM

As discussed in chapters 1 and 2, and in the present chapter (see above, “Inter-Site Movement”), CLNB engage in several different types of roosting activities 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. This 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”). At the same time, CLNB roosting has some similarities year round. The AZGFD (2014) specifically notes:

[CLNB] generally prefer to hang from the ceiling of caves and mines in groups of up to several hundred. Although they roost close to each other they are not usually touching or tightly packed as are the individuals of many other colonial bat species. If they do come into contact they become restless and move.

Roosting: Cold Season

Males and females roost together through the cold season in caves and underground mines—and in specific locations within these caves and mines—that provide a distinct set of thermal and morphological characteristics (see also chapter 4, “Temperature”). O’Shea et al. (2018) summarize CLNB cold-season roosting site affinities and behaviors as follows:

California leaf-nosed bats [in winter] require warm roost temperatures of about 23 to 27 °C or higher and do not drop body temperatures to very low levels or hibernate (Bradshaw, 1961; Bradshaw, 1962; Bell et al., 1986; Brown and Berry, 1991). However, this species can be somewhat heterothermic during winter and can reduce body temperature to about 26 °C and appear lethargic within roosts (Bradshaw, 1961, 1962; Leitner and Ray, 1964). They also are capable of surviving somewhat lower body temperatures for short periods in laboratory experiments (Reeder and Cowles, 1951), but the thermoneutral zone (where increased metabolism is not required to maintain a stable body temperature) is limited to body temperatures of 33 °C and above (Bell et al., 1986)...

...these bats regularly use naturally geothermally warm abandoned mines during cold months (Bell et al., 1986; Brown et al., 1993a,b). Use of different mine tunnels during summer and winter also has been reported in northwestern Arizona (Cockrum et al., 1996). During winter in the California desert, where

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night-time temperatures can drop as low as 0 °C, they are known to form colonies (about 200 bats or more in size) in just a few geothermally heated desert mines and will switch among these sites if disturbed (Bell et al., 1986).

Fewer than 20 geothermally warm winter roosts were known in California, all in abandoned mines (Brown et al., 1993b). The largest currently known winter colony in the U.S. is in an abandoned mine on Bureau of Land Management lands in southeastern California, where counts of up to 5,000 have been made since 2002 (Brown, 2013). Winter counts during emergence at another mine on Bureau of Land Management property in Arizona were as high as 3,500 in 2002, but fluctuated among years (Brown, 2013). Recent winter emergence counts of over 2,000 bats have been documented at another long-occupied and now gated mine in southeastern California (Brown, 2013). In southwestern Arizona, one mine in the Trigo Mountains held about 1,500 to 2,000 California leaf-nosed bats in recent winters, with up to 3,500 estimated in 2002 (Brown, 2013). The largest winter colony size reported in mines in the Agua Dulce Mountains of extreme southern Arizona was about 500 bats (Schmidt, 1999). California leaf-nosed bats do not form dense clusters in winter (Brown, 2013).

Roosting: Warm Season

Males and females mostly roost separately during the warm season, either in maternity colonies mostly occupied by reproductive females or in bachelor colonies occupied by males and non-reproductive females. As noted in chapter 1, mines may provide both summer and winter roosting areas, with the females moving closer to the entrance in the warm season, while the males continue to roost further back. The caves and underground mines used as warm-season roosts—and the specific locations used for roosting within these caves and mines—again provide a distinct set of thermal and morphological characteristics (see also chapter 4, “Temperature”). O’Shea et al. (2018) summarize CLNB warm-season roosting site affinities and behaviors as follows:

Vaughan (1959) described [warm-season] daytime roosts of California leaf-nosed bats in caves, deserted mine tunnels, and grottos in the Riverside Mountains of southeastern California, where these bats occurred in groups of from just a few to 100 or more. They were usually within 9 to 24 meters of entrances and did not seem to require completely dark retreats. Most of the tunnels observed to harbor bats were from 1.5 to 2.0 meters high and wide and five to over 30 meters deep. Bats were not observed roosting in tight clusters, but small groups of up to 20 individuals were observed with each bat slightly separated from adjoining individuals (Vaughan, 1959; see also Cockrum et al., 1996).

Maternity colonies form during summer in mines or caves where temperatures reach 27–32 °C (Brown and Berry, 1991). Banding studies suggest life-long fidelity to roosts but also show that movement to alternate sites may occur when the bats are disturbed (Brown et al., 1993a,b). Roosts in the Arizona portions of

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the range are in habitats that usually do not reach temperatures as low as in parts of California, and some of these caves and mines may be occupied year-round, whereas others may function principally as summer or winter roosts (Hoffmeister, 1986; Schmidt, 1999). At a well-studied roost in an abandoned mine near Silverbell in southern Arizona the population of up to 350 individuals consisted of about half males and half females during March and April, but in summer months females segregated into maternity colonies and males broke into small groups (Bradshaw, 1961) ... Seasonal changes in colony sizes have been reported in mines in the Agua Dulce Mountains of extreme southern Arizona, with near equal adult sex ratios in some but with a preponderance of females in others (Schmidt, 1999). The largest warm season colony in the latter study was about 200–300 bats. Recent (2000–2013) maximum counts at the four largest known summer colonies in abandoned mines in the Lower Colorado River area of southeastern California and southwestern Arizona ranged from about 100 to 500 individuals, predominantly males, whereas counts in spring can be much higher and include females (Brown, 2013).

Roosting: Interim

CLNB engage in two other types of roosting activity, which this CEM categorizes together as interim roosting: (1) seasonal aggregation for mating immediately prior to settling into cold-season roosting sites and (2) brief, temporary roosting during nocturnal foraging excursions, also called night roosting.

Mating aggregations occur in the same caves or mines used by CLNB during the subsequent cold season (Brown 2013). However, the literature reviewed for this CEM does not discuss whether the mating locations within these caves or mines differ in morphology or temperature from the locations used subsequently for cold-season roosting. The literature reviewed for this CEM (O’Shea et al. 2018) also suggests that at least some CLNB may move to other cold-season roosting sites after mating while others simply relocate to other portions of the same cave or mine. The mating locations within caves or mines presumably provide aerial and ceiling space for the mating displays (see chapter 1).

CLNB night roosts are natural or artificial features that simply provide overhead protection and a ceiling suitable for holding on while the bat consumes its prey. As a result, they may be only a few meters deep and include locations as diverse as the undersides of highway bridges, crevices in stacks of hay bales, shallow grottoes in canyon walls and banks of deep washes, and interiors of abandoned buildings. They may remain in their night roosts long enough to finish their meal before returning to foraging, or longer: As noted in chapter 2, CLNB exhibit two or more peaks of foraging activity over the course of each night during the warm season, minimally one before midnight, 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

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their maternity roost several times a night rather than using night roosts closer to their foraging area. CLNB do not appear to use temporary night roosting sites during the cold season but rather return to the warmth of their cold-season day-roosting site.

THERMAL STRESS

Exposure to air temperatures outside their ranges of tolerance presumably render CLNB pups and adults 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 CLNB activities along the greater Lower Colorado River Valley in Arizona, California, and Nevada is thought to be an adaptation to the thermal conditions they face at the northernmost extent of their range—a range that is in turn the northernmost among all species in the Phyllostomidae family. The species selects day-roosting sites in both the cold and warm seasons that provide a narrow temperature range both for adults and for their pups in maternity colonies. Individuals in both cold- and warm-season day roosts “... roost singly or in groups of up to several hundred individuals, hanging separately from the ceiling rather than clustering” (Brown 2013), suggesting that the air temperature in the roosting location provides sufficient warmth by itself without the need for any sharing of body warmth. Brown (2010) also notes that “In the winter, *Macrotus* will not exit the roost on very cold nights, preferring to remain in the warm mines that match their narrow thermal neutral zone.” The AZGFD (2014), in turn, notes that:

When temperatures drop to between 9° and 12 °C, they do not become torpid, but regulate their body temperature to between 18° and 20 °C. They can only survive these temperatures for a few hours. Sustained exposure to ambient temperatures less than 26 °C results in death. These bats rarely encounter such low temperatures for long periods within the underground caverns and desert conditions in which they live.

Chapter 4 (see “Temperature”) further discusses the available evidence on thermal affinities and tolerances among CLNB. 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 across the CLNB life cycle. 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 does not include this information. Critical biological activities or processes, in turn, may affect habitat elements. Specifically, CLNB drinking behaviors affect their exposure to chemical contaminants, and drinking, foraging, and both cold- and warm-season roosting behaviors affect their monitoring, capture, and handling. These links also do not appear in table 3.

Table 3.—Proposed habitat elements for the CLNB 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 →	Breeding	Chemical stress	Competition	Disease	Drinking	Feeding	Foraging	Inter-site movement	Maternal care	Mechanical stress	Predation	Roosting: cold season	Roosting: warm season	Roosting: interim	Thermal stress
Habitat element ↓															
Anthropogenic disturbance	X					X	X		X	X		X	X	X	
Arthropod community			X				X				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				
Water availability		X			X							X	X		

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Some of the habitat elements in this CEM differ in their details among life stages. For example, different species may prey on pup versus adult CLNB. 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 three other bat species in the Lower Colorado River Valley: western red bats, western yellow bats, and Townsend's big-eared bats (Braun and Unnasch 2020a, 2020b, 2020c). Except where noted, the information in this chapter comes from the most recent comprehensive species accounts by the AZGFD (2014), Brown (2013), the LCR MSCP (2016), NatureServe (2019), O'Shea et al. (2018), and the Western Bat Working Group (2019). 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 CLNB 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 CLNB roosting and foraging habitat.** This element refers to the existence and level of human disturbance of CLNB roosting habitat, including noise, intrusions, and physical contact with the bats.

Numerous publications have identified the disturbance of roost sites, including their entryways and immediate surrounding spaces, as a leading cause of the contraction of the geographic range of CLNB in the United States over the past 50 years (AZGFD 2014; Brown 2006, 2010, 2013; LCR MSCP 2016). The primary evidence for this causal relationship is the disappearance of CLNB from caves and mines in which they formerly roosted, following human disturbance of the cave, mine, or its immediate vicinity, including recreational use and the closure of mines for renewed mining or hazard abatement. The AZGFD (2014) specifically notes that "Loud noises in roosts may disorient the bats and also negatively affect reproductive success." Brown (2006) notes that CLNB "generally did not change roosts" following intrusions, while Huey (1925)

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describes disturbing CLNB at an unnamed mine near Potholes, Imperial County, California, and notes, “At first approach most of the bats flushed, going to the deeper levels of the mine.” Brown (2010) similarly notes for the Stonehouse Mine in the Mule Mountains southwest of Blythe, California, that “Local teenagers and young adults visit the site and litter the ground with broken beer bottles, ammunition casings and firecrackers. Before the bat gates were installed in 2006, the bats escaped disturbance by roosting down a deep and dangerous winze (internal shaft) inside the mine.” In any case, the susceptibility of CLNB to disturbance in their roosting sites has not been formally studied. The AZGFD (2014) consequently suggests a need for “historical studies of roost site use and disturbance.”

The literature reviewed for this CEM also reports that CLNB will abandon a roosting site following the destruction of foraging habitat in its vicinity. However, the literature does not report any instances of CLNB abandoning foraging areas simply because of human activity in these areas. Nighttime noise from infrastructure and human activities in developed areas may disrupt echolocation and thereby interfere with foraging among some bat species (Bunkley et al. 2015). However, the subject has not been investigated among CLNB, and the species shows no aversion to foraging or roosting in areas of intense human activity along the Lower Colorado River Valley, including foraging around the edges of active farmlands and roosting in stacks of hay bales. Similarly, their acute nighttime vision may allow them to detect and avoid mist nets (see below, this chapter, “Monitoring, Capture, Handling”), but the presence of mist nets in a locality does not appear to cause them to stop foraging in that locality.

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 CLNB roosting and foraging habitat.** The arthropods of concern include species that CLNB may consume (see chapter 3, “Foraging”), that may compete with or prey on CLNB, or that otherwise contribute to ecological dynamics in and around CLNB foraging or roosting sites.

Chapter 3 (see “Foraging”) discusses the range of arthropod species on which CLNB have been documented to feed based on field observations and analyses of stomach contents. The list includes Coleopterans (e.g., Carabidae, ground beetles, Cerambycidae, long-horned beetles, Meloidae, blister beetles, and Scarabaeidae, scarab beetles); Dictyopterans (e.g., cockroaches); Dipterans (true flies); Homopterans (cicadas); Hymenopterans, including flying ants; Lepidopterans (Cossidae, Noctuidae, Nymphalidae, Sphingidae, and their caterpillars); Odonates

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(dragonflies); and Orthopterans (grasshoppers, katydids, and crickets). The types and abundances of such arthropods available at night necessarily affect CLNB adult foraging success and nutrition.

There is a 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 CLNB 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). The CEM recognizes the possibility of arthropod predation on CLNB 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 along the Colorado River valley provide 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 Colorado River 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 can cause individual plant death within 2 years or more, with overall mortality rates up to 40%, depending on the site (Bean and Dudley 2018). The literature reviewed for

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this CEM 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 CLNB use or potentially could use as roosting habitat. As discussed in chapter 3 (see “Roosting: Cold Season, Warm Season, Interim”), CLNB use only caves and cave analogs for cold-season roosting and for warm-season maternal and bachelor roosting. They also use only caves and cave analogs as mating sites and may use caves and cave analogs as well as other features of the landscape for night (*aka* feeding) roosting. The LCR MSCP (2016) notes that:

Because the bats are restricted by specific roost requirements (such as temperature), their limited distribution causes them to form a small number of large colonies rather than several small ones. The loss of one colony can have a significant effect on the total population along the LCR (Brown 2006).

Natural caves used by CLNB 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. No deep natural caves are known to exist in the greater Lower Colorado River Valley (Berry et al. 2017; Brown 2006, 2010, 2013, *in press*; Maturango Museum and Brown-Berry Biological Consulting 2018). Cave analogs (*aka* cave-like structures or features) used by CLNB include overhangs and shallow cavities (*aka* rock shelters or grottoes) in cliffs, other bedrock surface outcrops, and the high banks of deep washes; the adits, airways, cavities, and passageways of inactive underground mines; cave-like cavities under bridges; crevices in stacks of hay bales; 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.” CLNB along the Lower Colorado River Valley are obligate users of abandoned underground mines for both cold- and warm-season roosting (Berry et al. 2017; Brown 2006, 2010, 2013, *in press*; Maturango Museum and Brown-Berry Biological Consulting 2018).

CLNB select caves and cave analogs for day roosting—and select specific locations within these features—based on four characteristics:

- The availability of one or more chambers with high ceilings and sufficient space for flight, with access to the open air through one or more passageways without constrictions that would impede CLNB flight between the chamber and the open air. According to O’Shea et al. (2018):

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Vaughan (1959) described daytime roosts of California leaf-nosed bats in caves, deserted mine tunnels, and grottos in the Riverside Mountains of southeastern California, where these bats occurred in groups of from just a few to 100 or more. They were usually within 9 to 24 meters of entrances and did not seem to require completely dark retreats. Most of the tunnels observed to harbor bats were from 1.5 to 2.0 meters high and wide and five to over 30 meters deep.

- The presence of air temperatures and humidities in the selected chamber(s) that remain stable within the suitable (thermal neutral) range for the species (see chapter 3, “Thermal Stress,” and below, this chapter, “Temperature”). Air temperature preferences differ between the cold and warm seasons.
- Low light levels in the selected chamber(s), neither completely dark nor subject to any direct daylight. The CLNB range of tolerance for light intensity may explain the limited range of distances from openings from which they may be found in caves and cave analogs. Brown (2013) notes that “Most [CLNB] diurnal winter roosts are in warm mine tunnels at least 100 meters long.” Anderson (1969) notes, “Although caves are the chief dwelling places this species also occupies mine tunnels and buildings, does not require complete darkness, is often found within 10 to 30 meters of the entrance of a tunnel or in partly lighted buildings.”
- One or more openings to the open air large enough for CLNB passage in flight. The literature reviewed for this CEM mentions that openings can be too small for CLNB passage (Brown 2013). Brown (2010) also mentions that, at the Jackpot Mine, “The main Jackpot adit (approximately 200 m long) is almost sealed by dirt washed down from above, leaving a 2-foot-diameter hole from which the bats emerge. When the mine was first visited in January 2002, almost 500 *Macrotus* exited after dark.” However, none of the other publications reviewed for this CEM provides measurements of opening size or shape for comparison.

Publications by Brown and co-authors (2010, 2013, *in press*; Maturango Museum and Brown-Berry Biological Consulting 2018) report that patterns of CLNB roosting site selection particularly in abandoned underground mines can affect the monitoring of roosting site use. These publications discuss difficulties and dangers at numerous mines for censusing or capturing CLNB due to features of mine location, construction, and internal hazards that prevent safe entry or internal movement by investigators, make it difficult to capture video, or make it difficult for investigators to observe exits and entries due to poor observation angles and/or too many openings.

CLNB in the cold season may roost in the same caves or cave analogs, where they also roost in the warm season, or in caves or cave analogs with similar overall

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characteristics. However, as noted below, this chapter (see “Temperature”) and chapter 3 (see “Thermal Stress”), they typically use different specific locations with different characteristics of temperature and humidity within these caves or cave analogs in each season.

CLNB night roosting sites, in turn, 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 (see chapter 3, “Roosting”). As a result, their characteristics vary widely.

All roosting sites used by CLNB share one additional common characteristic. As noted above, this chapter (see “Anthropogenic Disturbance”) and also in chapter 3 (see “Inter-Site Movement”), CLNB may abandon a cave or cave analog where they experience excessive disturbance, and they may not return for years after. As a result, caves and cave analogs in which CLNB maintain day-roost colonies are more likely to be sites with little or no anthropogenic disturbance.

CHEMICAL CONTAMINANTS

Full name: **The concentrations of chemical contaminants in the air, on ground or plant surfaces, in food items, and/or in surface waters in and around existing or potential CLNB roosting and foraging habitat.** This element includes chemicals that may contaminate arthropods on which CLNB feed, or contaminate surface waters where the bats may drink. In principal, such contaminants include biocides, mineral (e.g., metal, acid) leachates, and industrial wastes. As noted in chapter 3 (see “Chemical Stress”), chemical contaminants are recognized or suspected as threats to all bat species worldwide (Crichton and Krutzsch 2000; Hammerson et al. 2017; Hernández-Jerez et al. 2019; Tuttle and Moreno 2005; Voigt and Kingston 2016). The literature therefore also proposes that chemical contaminants could pose threats to CLNB in particular (Brown 2006; NatureServe 2019). However, the literature reviewed for this CEM provides little information on specific contaminants of potential concern for CLNB or their possible sources.

Based on the literature on other cave-dwelling bat species of concern in the Lower Colorado River Valley, particularly Townsend’s big-eared bats (Braun and Unnasch 2020c), and on the scant literature on chemical stress in CLNB, this CEM identifies the following as chemical contaminants of potential concern for CLNB:

- Soluble metals and mining industrial wastes due to roosting in abandoned underground mines, including in contaminated waters and dust within or associated with such underground mines (O’Shea et al. 2018; see

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chapter 3, “Chemical Stress”), as also suggested for Townsend’s big-eared bats (Gruver and Keinath 2006; O’Shea et al. 2018). Some metals may bioaccumulate in bat body tissues (Gruver and Keinath 2006), although the studies cited by O’Shea et al. (2018; see chapter 3, “Chemical Stress”) do not report bioamplification of lead or other elements in CLNB in abandoned underground mines at the Kofa National Wildlife Refuge, Arizona.

- 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 “Foraging”), CLNB forage actively in and around remnant native vegetation at the margins of irrigated agricultural fields where pesticides may be used to control insects. Further, aerial spraying of pesticides can result in contamination of adjacent, non-agricultural areas where the species may forage. As noted in chapter 3 (see “Chemical Stress”), a study of a small number of CLNB in Arizona and California in 1998 found organochlorines present “only at very low concentrations.” Nevertheless, the European Food Safety Authority (Hernández-Jerez et al. 2019) emphasizes that pesticide exposure poses a risk to all insectivorous bats worldwide.
- Radon, which 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 CLNB or their food resources along the Lower Colorado River Valley. A full review of the topic 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 CLNB roosting and foraging habitat.** Wildfires, prescribed fires intentionally set to manage vegetation and risks of wildfire, campfires, and fires caused by human negligence or malice may affect CLNB in any of four settings: (1) when fires occur in the vegetation patches where the species forages, (2) when fires occur in buildings that the bats may use as night roosting sites, (3) when 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

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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 CLNB 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 CLNB, 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; Mixan and Diamond 2016; 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 cottonwood and saltcedar in the Western United States.

Fire can affect CLNB foraging habitat along the LCR and, consequently, CLNB foraging activity, by altering vegetation, including the amount, height, and composition of canopy cover versus openings (Busch 1995). However, the exact ways in which fire can affect CLNB foraging habitat have not been studied, and the available evidence suggests no clear relationship. For example, a fire at the Cibola National Wildlife Refuge-Island Unit in August 2011 burned cottonwood-willow vegetation, and CLNB call minutes at the site subsequently increased in 2012 (relative to 2011) and then declined in 2013–15 (Mixan and Diamond 2016, 2017a, 2017b, 2018a, 2019a). Fires also burned in the Mittry Lake Wildlife Area in December 2014 and August 2015, and CLNB call minutes at the site declined in 2015 but increased again in 2016 (Mixan and Diamond 2016, 2017a, 2017b, 2018b, 2019a). Whether these dynamics reflect site-specific changes in the structure of foraging habitat and/or the availability of prey, or reflect larger-scale dynamics of where CLNB forage from year to year, is not known. Alternatively, the year-to-year variation in CLNB call minutes over these years at these sites may be merely random. CLNB produce very quiet echolocation calls that acoustic monitoring methods identify only with difficulty unless the bats call within close proximity to a microphone (see below, this chapter, “Monitoring, Capture, Handling”). Between 2010 and 2017, the overall rate of detection of call minutes per night at the Cibola National Wildlife Refuge-Island Unit peaked at only 0.11 call minutes per night in both 2010 and 2017, and at the Mittry Lake Wildlife Area, the overall detection of call minutes was 0.16 in 2010 and 0.09 in 2017 (Mixan and Diamond 2017b, 2018a). With such low incidences, it is not possible to determine if the variation between these two years is statistically significant.

Additionally, fire can affect the nocturnal monitoring of foraging CLNB. Specifically, fire can 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 CLNB.** CLNB 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”) CLNB can host the rabies virus, and infections can be fatal (Constantine 1979; Stuchin et al. 2018). Bradshaw and Ross (1961) identified four ectoparasites on CLNB in Arizona but did not assess their possible effects. The literature reviewed for this CEM provides no other information on specific bacterial, viral, fungal, or parasitic organisms that may infect CLNB or their possible effects, indicating a large gap in knowledge.

MATERNAL CARE

Full name: **The frequency, quantity, and quality of maternal care—nursing, cleaning, guarding, and thermoregulation—provided by reproductive female CLNB 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 CLNB pups.

MONITORING, CAPTURE, HANDLING

Full name: **The methods, frequencies, timing, and duration of (a) monitoring of CLNB habitat and (b) monitoring, capture, and handling of CLNB 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 CLNB, for example by disturbing them during roosting or causing mechanical stress and (2) the potential ways in which CLNB 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 Ellison et al. (2013), O’Shea et al. (2004), the National Park Service (NPS Institutional Animal Care and Use Committee 2016), and Sikes et al. (2016):

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- 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 equipment and/or hands 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 both from the procedures and, again, as they struggle to free themselves.
- The identification and tracking devices can themselves cause harm after being put in place. 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 specifically designed exclusively for that purpose (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 CLNB, 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 et al. 2012, 2013; Mixan and Diamond 2014a, 2016, 2017a, 2017b, 2018a, 2018b, 2019a, 2019b; Vizcarra and Piast 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 during capture, handling, and release, (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 hand nets or harp traps instead of mist nets under some circumstances, and (4) begin acoustic recording before sunset and end it after sunrise to ensure complete coverage of bat foraging activity. The protocols also identify the times of 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

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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). Finally, the protocols call for great caution when entering caves or other cave analogs where any bats may be roosting, including CLNB, to avoid disturbing them.

Conversely, several aspects of CLNB biology and behavior may affect the effectiveness of different methods of acoustic detection, counting, capture, and radio tracking. Specifically:

- Pregnant and lactating CLNB may be especially susceptible to injury and death from handling. Maturango Museum and Brown-Berry Biological Consulting (2018) report:

The transmitter weight and position can increase the energetic demands and alter maneuverability for bats at any time of the year (Aldridge and Brigham 1988). During pregnancy and lactation, the female bats have higher energy demands and forage longer without the addition of carrying a transmitter while foraging. A prior California leaf-nosed bat telemetry study resulted in the death of the both the lactating female and her pup (Brown et al. 1993). Consequently, bats have not been tracked during this reproductive period again.

- As noted in chapter 2, CLNB likely attain close to their adult weight by the time they are weaned and able to forage on their own. As also noted in chapter 2, adult CLNB almost always weigh more than 10 grams. As a result, the minimum size requirements for bats, to which a tracking device may be attached, should not bias the age range of CLNB that will be tracked. However, the evidence is not completely clear that year-one CLNB, post-weaning, necessarily have achieved their full adult size. This leaves open the possibility of an age bias among tagged CLNB.
- CLNB echolocation calls have very low amplitude (low decibels) compared to those of other bats along the LCR. CLNB are commonly described as “quiet” or “whispering” bats. As widely remarked by many investigators, CLNB echolocation calls consequently generally cannot be detected with acoustic monitoring equipment at distances greater than 15 m with a signal-to-noise ratio high enough to permit call discrimination (Broderick 2016; Brown 2006, 2010, 2013; Hill 2016, 2019a; LCR MSCP 2008; Mixan and Diamond 2014a, 2016, 2018a, 2018b, 2019a, 2019b; Mixan et al. 2013; NatureServe 2019; Tuttle 1998; Vizcarra 2011;

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Vizcarra and Piest 2010). The distances within which it is possible to discriminate CLNB calls may be even shorter at monitoring locations with higher densities of vegetation “clutter” (Mixan et al. 2012).

- CLNB echolocation calls can be difficult to distinguish digitally in acoustic monitor recordings from those of other species, such as the California myotis (*Myotis californicus*) and Yuma myotis, both of which occur widely in the Lower Colorado River Valley (Mixan and Diamond 2016; Mixan et al. 2012).
- CLNB echolocation abilities potentially may be great enough to enable them to detect and avoid mist net arrays, resulting in a deficit in mist-net captures noted by some publications (NatureServe 2019). Anderson (1969) notes:

*Echolocation [in CLNB], as in microchiropterans generally, involves laryngeally produced, nasally emitted, high frequency, pulsed sounds that are reflected, heard, and interpreted in such a way that the animal can avoid obstacles or locate food. Specifically, for *Macrotus*, obstacle avoidance is optimally effective for wires down to 0.27 mm. in diameter, and better than chance down to 0.19 mm. in diameter, in which case the wave length of the highest harmonic frequency, the fourth, is more than 10 times the wire diameter... Although their eyes are relatively large (for a microchiropteran) vision is unimportant in obstacle avoidance.*

Mixan and Diamond (2019b) further note:

A correlation of the acoustic and capture data being collected by Reclamation biologists at LCR MSCP conservation areas would further inform natural resource managers on bat activity and diversity at these sites, as it has been recorded that a combination of the methods was more successful in detecting bat species than either method alone (O’Farrell and Gannon 1999). Examining the capture data would be especially informative for California leaf-nosed and pale Townsend’s big-eared bats, which both emit low-amplitude calls and are difficult to detect acoustically.

Finally, Hill (2016; see also Hill 2019a) emphasizes:

This species [CLNB] ... has a relatively low capture rate in mist netting surveys along the lower Colorado River (LCR) (Calvert 2015a, 2015b); however, the species appears to be fairly common at several roost sites in the vicinity of the LCR (Brown 2010). The difficulty in remotely detecting this species using acoustic surveys and mist netting precludes using classic mark-recapture or telemetry techniques to understand even the basic demographics of the population along the LCR...

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- Foraging CLNB can and often do switch from echolocation to visual hunting, at which they are highly adept. As noted by O’Shea et al. (2018), “[CLNB] vision is very well developed compared to many other insectivorous bats, and they regularly interrupt echolocation and switch to vision to locate insects, particularly under moonlight conditions.” When they switch to visual hunting, they become undetectable by acoustic monitoring equipment.
- CLNB drinking behaviors appear to limit the frequency with which they may be observed, acoustically detected, or captured over water. Mist netting to capture bats in the Lower Colorado River Valley throughout the past two decades has included putting nets low across open water to capture bats when they come down to drink (Hill 2018). However, this only rarely results in the capture of any CLNB (Vizcarra and Piest 2010). Both acoustic monitoring and mist netting along surface waters in the Lower Colorado River Valley consistently result in low detections and captures of CLNB. This is part of a range-wide phenomenon noted by O’Shea et al. (2018), which notes (and discusses numerous supporting studies) that surveys of regional bat faunas in mist nets set over water seldom reported CLNB. Lactating females appear to be the only exception to this overall pattern. O’Shea et al. (2018) note, “One study found that 95% of 188 females taken in mist nets over water in southern Arizona during the maternity season were reproductive, although the great majority of these were lactating and thus had greater water needs (Schmidt, 1999), perhaps adding a positive bias.”
- CLNB and other bat species, such as Townsend’s big-eared bats, may roost in the same caves and mines and exit and enter nocturnally at the same times, making it difficult or impossible to conduct reliable exit or entry counts (Brown 2006, 2010, 2013, *in press*).

As noted above, this chapter (see “Caves and Cave Analogs”), patterns of CLNB roosting site selection particularly in abandoned underground mines can affect the monitoring of roosting site use. Brown and co-authors (Brown 2010, 2013, *in press*; Maturango Museum and Brown-Berry Biological Consulting 2018) report numerous cases in which features of mine location, construction, and internal hazards prevent investigators from safely entering or moving within the mines, capturing video, or observing CLNB exits and entries.

TEMPERATURE

Full name: The mean air temperature in and around existing or potential CLNB roosting and foraging habitat. This element refers to the average air temperature both within and outside individual caves or cave analogs that offer

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potential roosting locations for the species. Different locations within a cave or cave analog can have 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. Outside air temperatures, in turn, vary with the weather, season, altitude, and climate.

Bell et al. (1986) experimentally determined that adult CLNB have a thermal neutral zone of approximately 34 to 37 °C (lower and upper critical temperatures). Within this temperature zone, adult CLNB can maintain their internal body temperature with minimal metabolic or behavioral regulation; outside this temperature zone, adult CLNB must expend significantly more energy and engage in more elaborate behaviors to prevent discomfort or, in the extreme, hypo- or hyperthermia.

However, CLNB roost locations in caves and cave analogs exhibit a still very warm range but lower range of temperatures compared to the CLNB thermal neutral zone. Specifically, Brown (2010; see also Brown 2006, 2013) states:

*All known [CLNB] winter roosts in the deserts of California, Arizona and southern Nevada exhibit stable temperatures greater than 27 °C (80 °F) and relative humidities above 22%. The annual mean temperature in the California desert in the range of *Macrotus* is approximately 23 °C (73 °F) and the mean winter temperature is 14 °C (57 °F). The temperature of the occupied mines is warmer than the annual mean temperature, and the mines may be located in geothermally-heated rock formations (Higgins and Martin 1980).*

Brown (2013) also notes (see also chapter 3, “Thermal Stress”):

Since newborn [CLNB] are poikilothermic, the maternity colony is located fairly close to the entrance where temperatures range between 30–40 °C (86–100 °F). This allows the bats to use shallow, natural rock caves that would be too cold for a winter roost.

Additionally, the AZGFD (2014) states:

When temperatures drop to between 9° and 12 °C, [adult CLNB] do not become torpid, but regulate their body temperature to between 18° and 20 °C. They can only survive these temperatures for a few hours. Sustained exposure to ambient temperatures less than 26 °C results in death... Bell et al. (1986) suggest that these bats are able to exist in temperate desert areas because they minimize energy expenditure by using geothermally-heated winter roost sites with stable year-round temperature of about 29 °C and an "energetically frugal pattern of foraging that relies on visual prey location" and detection of prey-produced sounds.

The literature reviewed for this CEM does not address the apparent difference between the range of temperatures in which CLNB roost and the estimate of their

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thermal neutral zone determined by experiment. On the other hand, the literature does identify behaviors among CLNB adults that are hypothesized to help them cope with outside air temperatures beyond their apparent range of tolerance. Specifically, CLNB may: (1) relocate their day roosts to different caves or cave analogs or to different locations within the same cave or cave analog with more suitable temperatures (see chapter 3, “Roosting”) and (2) avoid exiting their cave or cave analog, or remain outside for only short periods, when outside air temperatures fall too low (e.g., less than 26 °C).

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 CLNB 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, woody vegetation greater than 2.0 m 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, CLNB appear to be affected by the tree and shrub vegetation in their environments in two general ways. First, the distribution of tree and shrub vegetation across the larger landscape around their day-roosting sites affects where CLNB forage, how far they must commute between their roosting sites and foraging areas, and the kinds of food items available in those foraging areas. Second, it affects conditions around the entrances to their roosting sites.

As obligate cave dwellers with narrow requirements for temperature conditions in the caves and cave analogs in which they can roost during the day, CLNB appear to find roosting sites where they can and forage in the vegetation communities available within 5 to 10 km of these sites. However, they exhibit some selectivity in where they roost, depending on some landscape conditions, and in where they forage among the vegetation communities available around their roosting sites. Specifically, Maturango Museum and Brown-Berry Biological Consulting (2018) notes:

The proximity of good foraging habitat appears to be a determining factor in roost selection. In recent surveys in the Panamint Mountains in California, mines with suitable temperatures were occupied by large maternity colonies

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(> 100 bats) only if they were within 2 miles (3.2 km) of a canyon with water (Dr. P. Brown, personal observation). Brown et al. (1994) determined by radio telemetry that this species on Santa Cruz Island bypassed lush introduced vegetation near their day roost, and traveled up to 3 miles (4.8 km) to feed in native oak and ironwood forest.

Otherwise, reviewing the literature on CLNB day-roosting site locations, Dudek (2015) notes that they are generally located today in creosote desert scrub and, at least in California, "... most are within 6 kilometers (4 miles) of desert washes containing ironwood (*Olneya tesota*), palo verde (*Parkinsonia* spp.), smoke trees (*Psoralea argemone*) and/or desert willows (*Chilopsis linearis*) (Brown, pers. comm. 2012)," but that, historically, "roosts (before development) near coastal areas of California were in chaparral or oak woodland." In turn, reviewing the literature on CLNB foraging habitat, Dudek (2015) finds that:

California leaf-nosed bats forage in riparian and desert wash areas in California, Arizona, and Nevada (Brown 2005; Huey 1925; Williams et al. 2006) and at tinajas (water-carved natural rock pools) and manmade tanks in southwestern Arizona (Rabe and Rosenstock 2005; Schmidt 1999). Williams et al. (2006) observed California leaf-nosed bats generally using riparian marsh, mesquite bosque, riparian woodland, and riparian shrubland without any apparent differential selection. The tinajas in the Rabe and Rosenstock (2005) study provided open flight approaches and were located near suitable roosting sites (cliffs and rocky canyons). For California, suitable foraging habitats are desert riparian, desert wash, desert scrub, desert succulent scrub, alkali desert scrub, and palm oases (Brown and Berry 2004; Zeiner et al. 1990). In the Sonoran Desert of Arizona (where desert trees are not confined to drainages), a greater percentage of the landscape is utilized by foraging bats (Brown et al. 1999; Dalton et al. 2000; Dalton 2001).

None of the literature reviewed for this CEM reports CLNB foraging over open ground or low herbaceous ground cover.

Acoustic monitoring and mist netting over the past two decades of CLNB along the LCR and Bill Williams River valley floors and radio tracking of foraging CLNB as they fly to and from their day roosts to forage (see chapter 3, "Foraging") provide some information on CLNB use of tree and shrub vegetation. Specifically, these studies document that CLNB in the greater LCR ecosystem forage more across the valley floors rather than along the dry washes that fringe these lowland settings. Across these lowland settings, as also discussed in chapter 3 (see "Foraging"), CLNB forage in both native and non-native tree and shrub vegetation, including in patches dominated by cottonwood-willow woodland, marsh, riparian shrubland, mesquite bosque, and saltcedar vegetation, as well as remnant native vegetation at the margins of irrigated agricultural fields. However, those CLNB that could be tracked across the Lower Colorado River

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Valley floor were found to focus their efforts on particular vegetation types when those types were readily available near their roosting site. Maturango Museum and Brown-Berry Biological Consulting (2018) report:

*The lush planted cottonwoods (*Populus fremontii*) and willows (*Salix gooddingii*) at the CVCA [Cibola Valley Conservation Area] and Cibola NWR [National Wildlife Refuge] Unit #1 are destinations for California leaf-nosed bats (#13a, #14a, #151, #15b, and #16b). These bats roosted in the Hart Mine and more arid day roosts to the east and south of the LCR on the YPG [Yuma Proving Grounds] from over 10 miles (16 km) away.*

Beyond this general information on the species composition of trees and shrubs in the areas where CLNB forage, the literature reviewed for this CEM provides little information on ways in which the vertical or horizontal structure of tree and shrub vegetation may affect CLNB foraging behavior. Increasing CLNB foraging activity (call minutes during acoustic monitoring) in LCR MSCP habitat conservation areas with maturing cottonwoods and willows (Broderick 2010, 2012a, 2012b, 2013, 2014, 2016; Calvert 2010a, 2010b, 2012a, 2012b, 2013, 2016a, 2016b; Hill 2018; LCR MSCP 2008; Mixan and Diamond 2018b, 2019b) does suggest that CLNB are attracted to the increasing canopy area and/or tree height at these locations. Otherwise, for example, the literature does not indicate if CLNB forage more around the edges of vegetation patches or throughout. In fact, the telemetry studies between 2010 and 2017 did not track a large number of CLNB. As a result, it is not possible to estimate what percentages of the CLNB along the Lower Colorado River Valley forage in different vegetative settings across the valley floor or along dry washes, or for what proportions of their time. It is only possible to securely estimate what vegetation settings CLNB use on a presence/absence basis (C. Ronning 2020, personal communication).

Tree and shrub vegetation potentially may affect CLNB 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 “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 they 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**

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existing or potential CLNB roosting and foraging habitat. This element refers to the range of vertebrate species known or suspected to interact with CLNB or its habitat along the Lower Colorado River Valley, particularly as prey, competitors, predators, or ecosystem engineers.

The literature reviewed for this CEM reports that CLNB may occasionally capture and consume lizards. Chapter 3 (see “Foraging”) addresses this interaction.

The literature provides only two direct pieces of evidence concerning vertebrate species that may prey on CLNB in the Lower Colorado River Valley or elsewhere. LCR MSCP (2016) cites a report of “... a dentary bone in barn owl (*Tyto alba*) pellets in Sonora, Mexico (Bradshaw and Hayward 1960).” As noted in chapter 3 (see “Predation”), investigators found a CLNB “... impaled on a barbed wire fence outside of a mine entrance near the Bill Williams River, likely by a loggerhead shrike.” Otherwise, the subject of which vertebrate species may prey on CLNB remains unstudied.

Predation information on bats in general (LCR MSCP 2016; Mikula 2015; Mikula et al. 2016) may provide guidance on species that potentially may prey on CLNB in the Lower Colorado River Valley. As noted in chapter 3 (see “Predation”), CLNB are vulnerable to predation in four settings: (1) in their day and night 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 CLNB forage and travel only at night, their vulnerability to predation in the latter three settings occurs only at night.

Owls that potentially could prey on CLNB at night along the Lower Colorado River Valley include not only the barn owl, confirmed by one observation (see above), but also the 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 CLNB has not been studied.

CLNB often roost during the day in the same caves and mines also used by Townsend’s big-eared bats (see above). Information on predation on the latter species within and at the entrances to their roosting sites therefore may provide some guidance on potential predators on CLNB in these same settings. Gruver and Keinath (2006) specifically report the following for Townsend’s big-eared bats:

*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*

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*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.*

The possibility of predation on CLNB by a loggerhead shrike (see above) requires further examination. This species of bird is not known to forage at night but conceivably could capture CLNB immediately at dusk or dawn as the bats exit or return to their day roost. Other birds conceivably could prey on CLNB in the same circumstances. However, the subject is unstudied.

LCR MSCP (2016) notes that “Known bat predators include domestic cats, dogs, birds of prey, snakes, raccoons, weasels (*Mustela* spp.), predatory song birds (Passeriformes), frogs (Anura), large spiders (Araneae), and even other bats (Fenton 2001).” Based on their diets and foraging ecology, other potential vertebrate predators on CLNB 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* (J. Hill 2019b, 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. CLNB historically roosted in abandoned underground mines in these mountains and continue to do so today (Berry et al. 2017; Brown 2006, 2010, 2013, *in press*; Maturango Museum and Brown-Berry Biological Consulting 2018).

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

The literature does identify at least three vertebrates that may affect CLNB 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) above, this chapter (see “Tree and Shrub Vegetation”):

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

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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 (Mueller 2006; Hautzinger 2010; 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 salt cedar (*Tamarix* spp.) 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 CLNB roosting and foraging habitat, and the depth of the water table in these settings. Efforts to capture bats during systematic investigations along the Lower Colorado River Valley over the past two decades have regularly included the placement of mist nets over surface water bodies to capture bats when they fly down to drink (see list of publications on bat monitoring in the Lower Colorado River Valley in chapter 1, e.g., Brown 2006; Hill 2018). These efforts have not resulted in the capture of any CLNB. O’Shea et al. (2018) reviewed a large set of literature on efforts to capture CLNB in Arizona, California, and Nevada and concluded, “Surveys of regional bat faunas in mist nets set over water have seldom reported this species, perhaps because the bats are restricted in roosting and foraging habits, generally do not disperse far from roosts, and are maneuverable fliers that readily avoid capture.”

Alternatively, the low success rate for capturing CLNB over water may be related to other aspects of their ecology. As noted in chapter 1, and also chapter 3 (see

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“Chemical Stress”), CLNB adults are able to strongly concentrate urine, and thus conserve water, and feed on larger insects, and even lizards, from which they are able to obtain a significant fraction of their daily water needs. As a result, as noted by the AZGFD (2014), “Some individuals in captivity have been reported to go for at least 6 weeks without drinking water (Lu and Bleier 1981).” CLNB pups, in contrast, obtain all of their water through nursing, which may place higher demands for water consumption in lactating (adult) females.

It is also useful here to repeat the quotation from Brown and co-authors (Brown 2010, 2013, *in press*) presented earlier in chapter 3 (see “Drinking”):

*Open water for drinking does not appear to be a criterion for roost selection since some roosts are located over 50 km (31 miles) away from the nearest known water source. The bats exist primarily on moisture contained in the juicy insects that they consume (Bell et al., 1986). Radio telemetry studies designed to determine foraging habitat of *Macrotus* in the California and Arizona deserts indicated that the bats did not visit areas of open water (Brown et al., 1993; Brown et al., 1999; Dalton et al., 2000). Schmidt (1999) did mist net *Macrotus* (especially lactating females) over water sources in the southern Arizona desert. *Macrotus* are regularly netted at a pool along the Bill Williams River (Brown and Berry, 2003).*

Similarly, following a systematic survey of bat foraging habitat use in relation to multiple environmental variables recorded at individual acoustic monitoring stations, Vizcarra (2011; see also Vizcarra et al. 2010) found:

Although California leaf-nosed bats are known to use water sources, they are apparently not dependent on them and can derive their water requirements from their prey (Brown et al. 1993). In addition, the wide availability of water along the LCR would make this relationship difficult to detect. My findings that this species was more likely to occur further from the river may reflect the fact that California leaf-nosed bat roosts and foraging habitat are typically in upland desert areas (Brown et al. 1993), relatively far from the river.

Water availability also may not predictably affect CLNB exposure to chemical contaminants. O’Shea et al. (2018), discussing the findings of high concentrations of lead in CLNB roosting in abandoned underground mines at the Kofa National Wildlife Refuge, Arizona (see above, this chapter, “Chemical Contaminants”), note that the study did not find evidence the lead came from the bats drinking in contaminated water at the mine. Rather, the study “... found very high lead levels in the soils from the floor of these mines and hypothesized that the leaf-nosed bats were accumulating lead through grooming lead particles from dust on the fur and from inhaling lead-contaminated dust within the mines.”

Water availability potentially may affect CLNB indirectly by affecting the arthropod and vertebrate communities and tree and shrub vegetation across the

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landscape, including across existing and potential foraging areas as well as 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 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 the CLNB in the LCR ecosystem and the habitat elements they directly affect

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

Habitat element →	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
Controlling factor ↓										
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		X							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.

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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 (LCR MSCP 2004) directs the program to carry out conservation measures to meet the biological needs of 8 threatened or endangered species and 19 other covered species, and to potentially benefit 5 evaluation species. CLNB 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 CLNB (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 CLNB 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

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National Wildlife Refuge and the Cibola National Wildlife Refuge-Island Unit (J. Hill and C. Ronning 2018, joint personal communication; Hill 2018; 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 CLNB foraging habitat, including actions to affect the taxonomic composition, abundance, condition, and spatial distribution of vegetation.** The HCP (LCR MSCP 2004) directs the LCR MSCP to carry out conservation measures to meet the biological needs of 8 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, disking and plowing, and the application of herbicides (LCR MSCP 2004, 2014, 2018a). Agencies and irrigation and drainage districts may also remove vegetation to maintain roads and canals under their authorities.

As noted in chapter 1, CLNB 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, *in press*; 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 day-time roosts in caves and mines located largely outside the planning area to do so. The LCR MSCP therefore recognizes the CLNB that use the planning area as an LCR population. Consequently, 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.

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

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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 Lower Colorado River 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 surrounding, inactive industrial area and 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 (AZGFD 2014; Brown 2006, 2010, 2013, *in press*; LCR MSCP 2016; NatureServe 2019; O'Shea et al. 2018; Tobin and Chambers 2017).

Properly designed and installed gating (*aka* bat-compatible gating) of cave and mine entrances appears to be widely recognized as an effective practice to eliminate unauthorized intrusions by people into the day-roosting sites of CLNB (AZGFD 2014; Brown 2006, 2010, 2013, *in press*; LCR MSCP 2016; NatureServe 2019; O'Shea et al. 2018; Tobin and Chambers 2017). Bat-compatible and less elaborate gates and fences have been installed across the openings to numerous day-roosting sites surrounding the LCR and Bill Williams River valleys. These efforts have usually either not affected CLNB use of these sites or have been followed by increases in use (Brown, *in press*). However, the picture is not completely consistent. Combined spring outflight counts of CLNB, Yuma myotis, and Mexican free-tailed bats from the Islander Mine complex from 2002 through 2016 have been consistently lower since a gate was installed in March 2013 (Brown, *in press*). However, the outflight counts for this mine do not distinguish among the three species, and CLNB is the least common of the three here. The mine is located 1 km west of Lake Havasu in the Whipple Mountains, California. Similarly, combined spring outflight counts of CLNB and Yuma myotis from the Eureka Mine complex from 2002 through 2016 also mostly show lower numbers after a cupola was installed over the two upper shafts in 2006 (the two lower adits were gated in 1995) (Brown, *in press*). However, the counts first increased in 2007 before dropping to historically low levels, and they do not

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distinguish between the two species. Yuma myotis is the more common of the two at this complex, which is located in the Chocolate Mountains on the Arizona side of the Imperial National Wildlife Refuge. In any case, the literature reviewed for this CEM identifies improper gating as a potential threat to CLNB numbers and distribution overall (AZGFD 2014; NatureServe 2019).

Summarizing the literature, O'Shea et al. (2018) state:

California leaf-nosed bats will roost in mines fitted with bat-compatible gates and, as noted in the following examples, properly designed and installed gates are an effective way of protecting this species from human disturbance. The National Park Service has used bat-compatible closure methods at abandoned mines occupied by this species at Lake Mead National Recreation Area and Joshua Tree National Park (Burghardt, 2000). An abandoned mine on Bureau of Land Management property in southeastern California housing a wintering colony of about 2,000 of these bats has been successfully gated, resulting in increased use by bats (Henry, 2002), as has another mine in the area that was gated in 2006 (Brown, 2013). In Arizona, a wintering colony of about 400 individuals in an abandoned mine being encroached upon by suburban sprawl near Phoenix has also been protected with bat-friendly gating (Corbett, 2008), as has a mine in the Trigo Mountains of the Lower Colorado River area that continues to serve as both a winter roost and a lek mating area in autumn since gating in 2007 (Brown, 2013). In an analysis of the effects of bat gates on multiple species, Tobin (2016) concluded that California leaf-nosed bats continued using gated mines over the long-term, tolerated various gate designs, and that the landscape location and structural complexity of a mine were better predictors than gate characteristics in determining if this species would continue using a site after gating.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

Full name: The introduction and management of nuisance species that potentially may interact with CLNB in and around existing or potential CLNB 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 includes both intentional and accidental introductions *other than* intentional introductions for recreation such as non-native fish and game species. Management activities may include efforts to control the spread of nuisance species through interdiction and education and 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

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involved in nuisance species management along the LCR and Bill Williams River valleys include the Bureau of Land Management; State of Arizona; USFWS; 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 CLNB attract recreational visitors as well. These visitors potentially can travel far enough into caves or underground mines to reach interior areas where CLNB gather. 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 CLNB as foraging habitat.** The lands surrounding LCR MSCP habitat conservation areas and other protected areas—particularly surrounding locations used or potentially usable by CLNB 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, disking 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 CLNB foraging habitat.** This controlling factor specifically concerns the water storage-delivery system within the LCR MSCP planning area. The filling of Lake Mead (1935–38) and Lake Mohave (1951) inundated some historic CLNB roosting sites located within the lands that were later included in the LCR MSCP planning area. Depending on lake water levels, regulated independently of the LCR MSCP, the shorelines of the two lakes today provide watercraft landing sites from which visitors can more or less easily reach other roosting sites (Brown 2010, 2013, *in press*; O’Farrell 1970). All other caves and underground mines potentially available to CLNB 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 (LCR MSCP 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 USFWS, 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 two sections, each presenting the CEM for a single life stage for CLNB. 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

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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

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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.

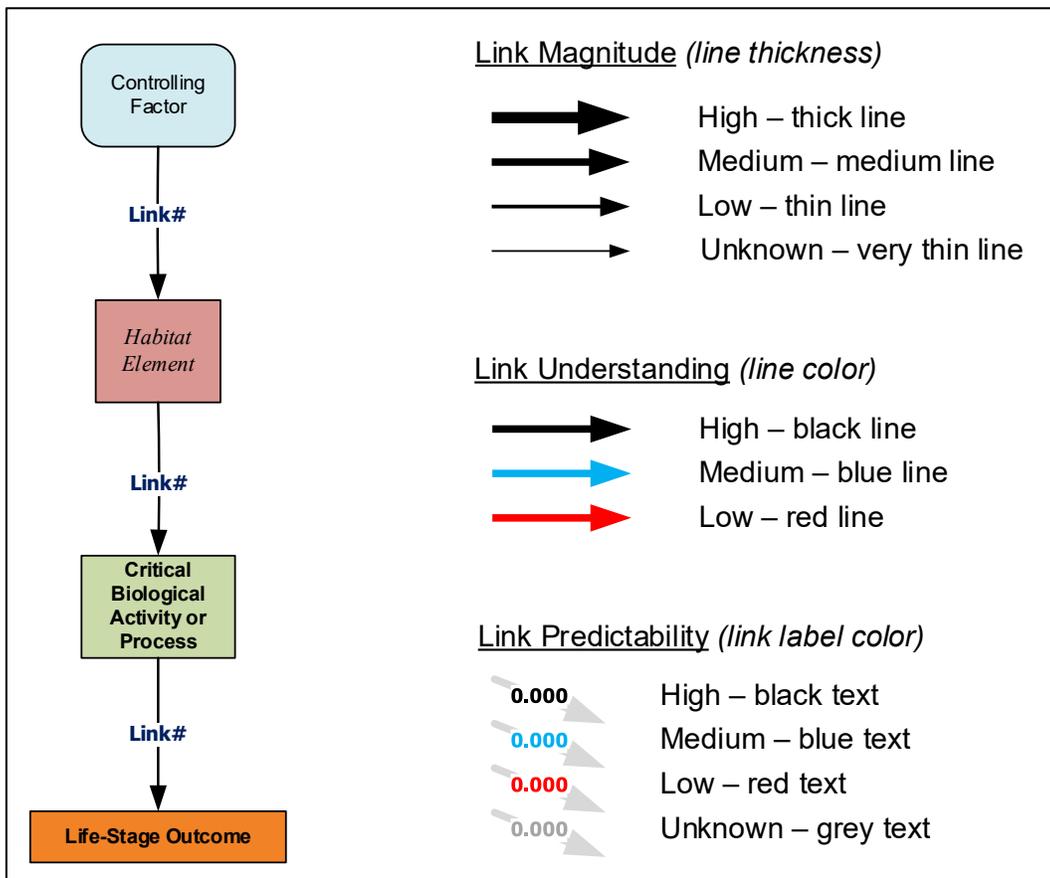


Figure 2.—Diagram conventions for LCR MSCP species CEMs.

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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. 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 both CLNB 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 the pup (almost always just one per mother) in a maternity colony, mostly from early May through early June, but overall from mid-May to early July after a gestation period of almost 9 months. The stage ends when the pup is weaned after approximately 1 month, at which time it begins foraging for itself. This life stage has two life-stage outcomes (see figure 1): pup growth and pup survival. CLNB are born weighing approximately 25 to 30% their adult weight and apparently reach roughly their full adult size and skeletal maturity by the time they begin foraging for themselves. They thus achieve a three- to fourfold increase in body mass during this life stage. The literature reviewed for this CEM provides no data on survival rates. Figure 3 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 CLNB pups depends on the maternal care they receive, beginning with the selection of the 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.

Effects of Life-Stage Outcomes on Each Other

This CEM proposes that pup growth affects pup survival but with unknown magnitude. As noted above (see also 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 CLNB 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 CLNB or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is rated as low.

Effects of Critical Biological Activities and Processes on Life-Stage Outcomes

This CEM identifies seven critical biological activities or processes affecting one or both outcomes for this life stage: chemical stress, disease, feeding, mechanical stress, predation, warm-season roosting, 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.

This CEM proposes link magnitudes for the effects of four critical biological activities or processes on pup survival or growth. Specifically, it hypothesizes that chemical stress, feeding success, and thermal stress all have high-magnitude direct effects on both pup growth and pup survival; and that mechanical stress has a low-magnitude effect on pup survival. The latter rating reflects the likelihood that most injuries to a CLNB pup will likely result directly in mortality rather than any persistent mechanical stress. CLNB pups, like all bat pups, are fragile. The effects of the other three critical biological activities or processes on pup survival or growth, and the effects of mechanical stress on pup growth, are rated as having unknown magnitude, again reflecting large gaps in knowledge.

Effects of Critical Biological Activities and Processes on Each Other

This 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, it 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. The CEM rates the magnitude of the effect of predation on mechanical stress as low, again reflecting the likelihood that most injuries to a CLNB pup will likely result directly in mortality rather than any persistent mechanical stress. Otherwise, this CEM identifies the magnitudes of all 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. This CEM proposes these links based on suggestions in the published literature on CLNB and on basic principles of bat biology.

Effects of Habitat Elements on Critical Biological Activities and Processes

This CEM identifies three habitat elements with direct, mostly high-magnitude effects on one or more of the seven critical biological activities or processes that shape this life stage. Most importantly, it proposes that maternal care affects pup growth and survival in five ways: (1) through the provision of food to each pup (high magnitude, high understanding), (2) through maternal selection of the maternity roosting location (high magnitude, medium understanding), (3) through various behaviors that protect the pup from thermal stress (high magnitude, medium understanding), (4) through behaviors that try to protect the pup from predators (high magnitude, low understanding), and (5) through grooming to remove ectoparasites from the pup and nursing, which may convey some initial immunity to pathogens (unknown magnitude, low understanding). This CEM proposes the last of these five links based on suggestions in the published literature on CLNB and on basic principles of bat biology.

This CEM identifies the vertebrate community and the tree and shrub community at the openings to maternity roosting sites as habitat elements with high-magnitude effects on a single 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 CLNB, including pups, in the maternity roosts. The size, shape, and other characteristics of tree and shrub vegetation around cave and mine entrances potentially could affect predation rates on CLNB in these settings through their effects on the amount and types of cover

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they provide for predators or the amount of clutter they create that affects CLNB abilities to detect predators. However, both subjects are unstudied for CLNB. This CEM proposes these two relationships based on suggestions in the published literature on CLNB and on basic principles of bat biology.

This CEM identifies three other habitat elements as having low- or medium-magnitude effects on the critical biological activities or processes that shape this life stage. It proposes that anthropogenic disturbance may affect both mechanical stress (medium magnitude, low understanding) and feeding (low magnitude, low understanding), and that temperature may affect thermal stress (low magnitude, medium understanding). The two effects of anthropogenic disturbance are unstudied for CLNB and proposed in this CEM based on suggestions in the published literature on CLNB and on basic principles of bat biology. The effect of temperature on thermal stress for bat pups is widely acknowledged in the literature, even if unstudied for CLNB, but its magnitude is mediated by maternal care.

Finally, this CEM identifies five habitat element that may 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. Infectious agents presumably may affect disease incidence; exposure to chemical contaminants presumably may result in chemical stress; fires (fire regime) within and around the entrances to the mines used as maternity sites have the potential to cause thermal stress; monitoring, capture, and handling of pups has the potential to cause them mechanical stress; and the arthropod community within the mines used as maternity sites affects the rate of predation on pups. Except for the possible effects of monitoring, capture, and handling, these five links are all rated as unknown for link magnitude and low for understanding. The possible effect of monitoring, capture, and handling is rated as unknown for magnitude but high for understanding: It is well known that intrusions into maternity roosts and handling of pups or their mothers can harm CLNB pups, but there are no data available from which to estimate rates of injury. Further, modern monitoring protocols are designed to minimize harmful effects.

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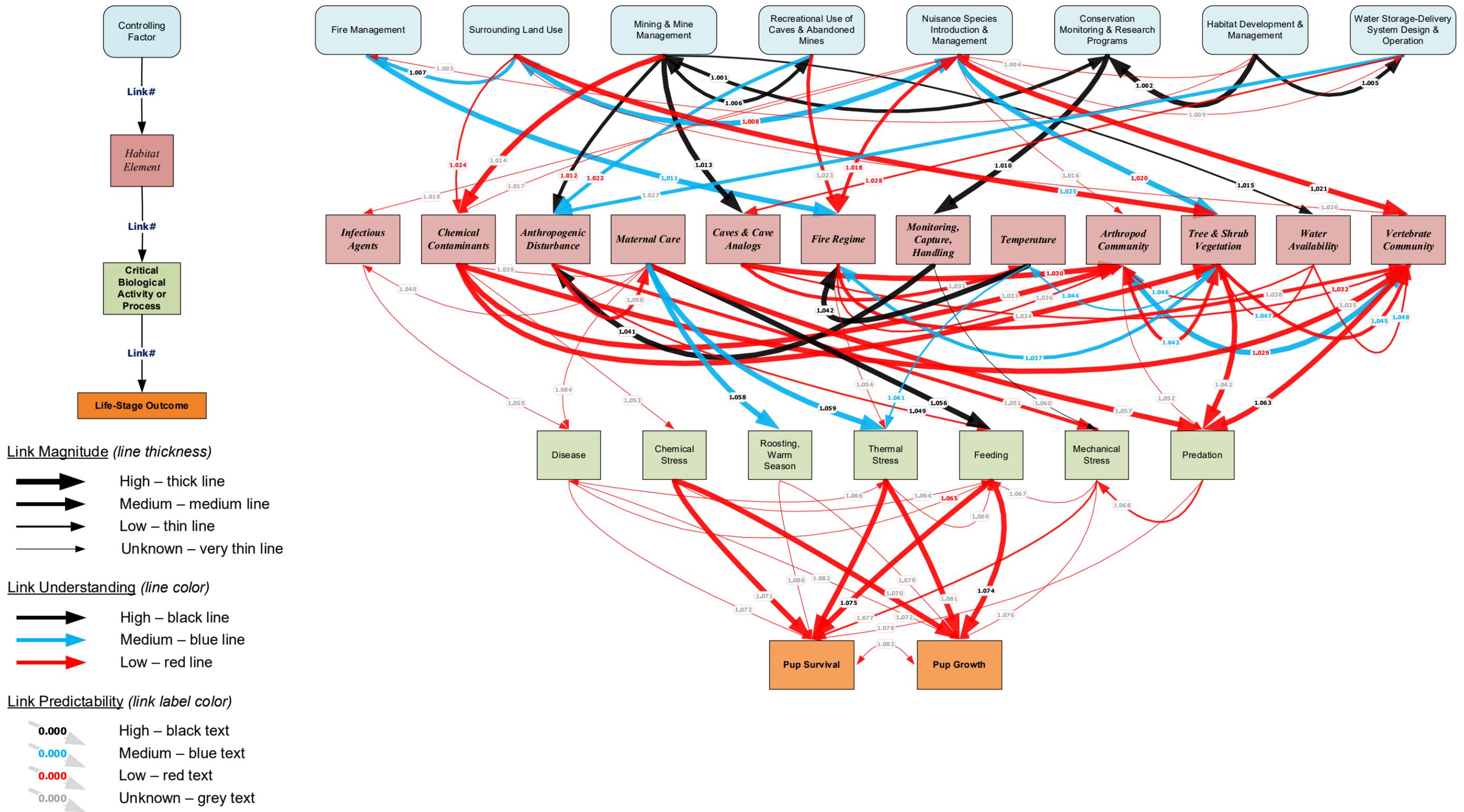


Figure 3.—CEM master diagram for CLNB life stage 1 – pup life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LIFE STAGE 2 – ADULTS

As described in chapter 2, the CLNB adult life stage begins when pups are weaned and become volant and they begin foraging for themselves. They do not necessarily become sexually mature at this time. An unquantified but apparently large proportion of adult females breed in the first autumn following their birth, while all other females and all males become reproductively active only in their second year. Limited observations indicate that individual CLNB lives can span up to 15 years in the wild.

The CEM for the CLNB adult life stage has three life-stage outcomes (see figure 1): adult growth, adult survival, and adult fertility. The literature reviewed for this CEM provides no information on whether adults continue to grow larger as they age. However, growth also involves the maintenance of seasonal fat reserves and strength and seasonal physiological changes to support reproduction and maternal care. No data are available on adult annual survival rates. A limited number of studies have found that approximately 95% of females may be reproductive in a given year. Figure 4 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.

Effects of Life-Stage Outcomes on Each Other

Similar to the CEM for the pup life stage, the CEM for the CLNB adult life stage proposes that adult growth affects adult survival but with unknown magnitude. As noted above (see also 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 CLNB 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 CLNB 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 survival and adult growth both affect fertility but with high magnitude. Theoretically, growth—i.e., maintenance of body mass and fat reserves for reproduction—is crucial to CLNB fertility. This CEM also proposes that CLNB adult growth also affects the critical biological activity or process, breeding, by determining whether individual females are even able to participate in reproduction in a given year in the first place. And logically, only adults that survive from one reproductive season to the next can continue to reproduce. These relationships should be strong, based on

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core biological principles. However, no studies have addressed the topics specifically for CLNB or any closely related species. As a result, the magnitudes of these links are rated as high but with low understanding.

Effects of Critical Biological Activities and Processes on Life-Stage Outcomes

This CEM identifies six critical biological activities or processes that directly affect adult survival: chemical stress, disease, foraging, mechanical stress, predation, and thermal stress. However, only four of these—chemical stress, foraging, predation, and thermal stress—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—including hydration stress, which this CEM recognizes as a type of 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 CLNB 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 and from exposure to persistent agricultural pesticides. Some metals and pesticides or their residues may bioaccumulate in bat body tissues. Only a single study has examined CLNB body loads of such chemicals, but not specifically in the Lower Colorado River Valley (although nearby, at the Kofa National Wildlife Refuge), and found no evidence of impaired health. However, the impacts have been identified as a topic of concern. At the same time, CLNB possess several physiological and behavioral adaptations for obtaining and conserving water in their hot, arid environment. Their risk of hydration stress appears to be low. However, no data are available on CLNB survival rates in either life stage, and the literature reviewed for this CEM does not discuss the possible relative impact of different possible causes of CLNB mortality. Further, 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.

Adult bats that do not forage effectively simply die from starvation, die from complications of other sources of stress, or suffer higher levels of predation. However, the literature reviewed for this CEM does not address the possibility of variation in CLNB foraging success or its possible consequences. Further, as noted above, 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.

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Similarly, vertebrates that could prey on CLNB 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 CLNB adult survival in the greater LCR ecosystem or elsewhere. Further, the literature reviewed for this CEM does not address predation on CLNB, and as noted above, 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 CLNB adults. At the same time, it recognizes that the subject remains unstudied in the Lower Colorado River Valley or elsewhere, necessitating a link rating of low for understanding.

As discussed in chapter 3, the entire annual cycle of CLNB activities along the greater Lower Colorado River Valley in Arizona, California, and Nevada is thought to be an adaptation to avoiding the potential for thermal stress that the species faces at the northernmost extent of its range—a range that is in turn the northernmost among all species in the Phyllostomidae family. The adaptation does not include hibernation, but it does include roosting in caves and mines that provide narrow ranges of warm, stable air temperatures in the cold and warm seasons and limiting their foraging activities to at most approximately 2 hours during cold weather. The inflexibility of these behaviors suggests that thermal stress has played a significant role in natural selection on the species. However, the literature reviewed for this CEM does not address the possibility of variation in thermal stress on CLNB or its possible consequences. Further, again as noted above, 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.

This CEM identifies five critical biological activities or processes that directly affect CLNB adult growth: chemical stress, disease, foraging, mechanical stress, and thermal stress. However, only three of these, chemical stress, foraging, and thermal stress, 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—including hydration stress, which this CEM recognizes as a type of 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. As noted above, this chapter, the literature on CLNB specifically mentions the possibility of impaired health from exposure to soluble metals and mining industrial wastes due to roosting in abandoned underground mines and from exposure to persistent agricultural pesticides. As also noted above, only a single study has examined CLNB body loads of such chemicals, and not specifically in the Lower Colorado River Valley (although nearby, at the Kofa National Wildlife Refuge), and found no evidence

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of impaired health. However, again, the impacts have been identified as a topic of concern. At the same time, as noted above, CLNB possess several physiological and behavioral adaptations for obtaining and conserving water in their hot, arid environment. Their risk of hydration stress appears to be low. However, no data are available on CLNB adult health or growth rates. This CEM hypothesizes that chemical stress poses potentially serious risks on CLNB adult growth but 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 CLNB fertility. This CEM recognizes this relationship by including a high-magnitude effect of chemical stress on another critical biological activity or process, breeding, as discussed below.

This CEM proposes a strong effect of foraging success on CLNB adult growth simply because obtaining food is essential for growth in any species. As noted above, growth for CLNB 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 CLNB adults is unknown either in the Lower Colorado River Valley or elsewhere. The CEM therefore rates the link as low for understanding.

This CEM also proposes a strong effect of thermal stress on CLNB adult growth. The reasoning for this hypothesis parallels that for the hypothesis, above, that thermal stress has a potentially strong effect on CLNB adult survival. However, the incidence of harm or impaired growth from thermal stress among CLNB adults is unknown either in the Lower Colorado River Valley or elsewhere. The CEM therefore rates the link as low for understanding.

The CEM for the CLNB 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 CLNB adults in breeding and their breeding success (fecundity, which is affected by maternal care, as discussed below), together with adult survival, determine CLNB fertility. However, there are no data available on breeding success rates for CLNB in the Lower Colorado River Valley or anywhere else. Consequently, this CEM rates understanding as low for this relationship.

Maternal care likely also has a large effect on CLNB reproductive success. In the extreme, for example as seen in other bat species such as Townsend's big-eared bats (O'Shea et al. 2018), disruptions to maternity colonies potentially could cause individual lactating females or even entire maternity colonies to abandon their pups and flee, resulting in complete reproductive failure of that colony for the year. Anecdotally, investigators do not report such extreme events at CLNB maternity colonies. However, there are no systematic data available on the subject for CLNB in the Lower Colorado River Valley or anywhere else. Consequently, this CEM rates understanding as low for this relationship.

Effects of Critical Biological Activities and Processes on Each Other

This 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. The CLNB conceptual ecological model in fact proposes 34 such causal relationships among critical biological activities and processes for the adult life stage. Further, four of these links are bi-directional; in effect, this CEM thus proposes 38 causal relationships among critical biological activities and processes for the adult life stage that may compound the effects of these critical biological activities and processes on adult growth, survival, and fertility.

Twenty three of the resulting 38 links between individual critical biological activities and processes in the CLNB adult life stage are proposed based on suggestions in the literature on CLNB and on basic principles of bat biology and are rated as unknown for magnitude and low for understanding. The CEM for the CLNB adult life stage suggests stronger magnitude (high, medium, or low) ratings for the other 15 links among critical biological activities and processes as follows:

- The CEM proposes that drinking success helps prevent or reduce chemical stress since the CEM recognizes hydration stress as a form of chemical stress. The link has high magnitude but medium understanding; studies have investigated CLNB abilities to conserve water and obtain most of their moisture from their diet.
- The CEM proposes that foraging success for pregnant and nursing females affects their success in breeding and in providing maternal care with high magnitude. 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 also proposes that foraging success for all adult CLNB affects their drinking behavior. As noted above, CLNB in the wild appear to obtain most of their moisture through their diet. The greater their success in doing so, the less they have to rely on drinking directly from surface waters to meet their moisture needs. The link from foraging to drinking is rated as medium for understanding.
- The CEM proposes that breeding success also depends, with high magnitude, on successful selection of a suitable roosting site by reproductive females for both the cold and warm seasons. CLNB reproductive females become pregnant in autumn but are able to metabolically delay embryo development through the cold season, after which they move to maternity sites to complete their pregnancies and rear their single pups. Successful selection of both cold- and warm-season

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roosting sites includes selecting sites with the right range of stable temperatures and suitable protection from hazards. 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 link from cold-season roosting to breeding is rated as low for understanding due to a lack of systematic study of the subjects in the literature on the species in the greater Lower Colorado River Valley or elsewhere. In contrast, the link from warm-season (maternity) roosting to breeding is rated as high for understanding; this is a well-understood relationship.

- The CEM proposes that drinking and maternal care reciprocally affect each other with medium magnitude. CLNB lactating mothers have greater needs for water than do other adult CLNB. As a result, they appear to meet more of their moisture needs through drinking, and the more success they have in doing so, the better they are able to produce milk for their single pups. The link is rated as medium for understanding; the relationships are moderately documented in the literature reviewed for this CEM.
- The CEM proposes that the risks CLNB experience or anticipate from predation affect their foraging behaviors specifically by causing them to avoid foraging when moonlight is strong. However, the link is rated as low for understanding due to a lack of systematic study of the subject in the literature on the species in the greater Lower Colorado River Valley or elsewhere. The relationship between lunar phobia and predator avoidance is considered only a hypothesis.
- The CEM proposes that both cold- and warm-season roosting site selection, together with risks of thermal stress, may affect CLNB inter-site movement, with medium magnitude. The three links are rated as low for understanding due to a lack of systematic study of the subjects in the literature on the species in the greater Lower Colorado River Valley or elsewhere.
- The CEM proposes that CLNB interim roosting behavior, specifically the selection and use of mating (lek-like) sites affects their breeding behavior, with medium magnitude. It is not clear that all mating takes place at such interim roosting sites or that such roosting sites are necessarily different from the roosting sites where CLNB spend the cold season. The link is rated as low for understanding due to a lack of systematic study of the subject in the literature on the species in the greater Lower Colorado River Valley or elsewhere.

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- Finally, the CEM proposes that two critical biological activities and processes for the adult life stage affect other critical biological activities and processes for the adult life stage with low magnitude. It proposes that some competition for food items could exist among CLNB with each other and between CLNB and other vertebrates. However, bats are thought to partition their resource use highly effectively, such that competition is minimal. The link is rated as low for understanding due to a lack of systematic study of the subject in the literature on the species in the greater Lower Colorado River Valley or elsewhere. The CEM also proposes that CLNB drinking behaviors could expose them to predation, specifically when they swoop low to drink. However, CLNB apparently obtain most of their moisture through their diet, and this reduces the magnitude of the latter proposed link. The link is rated as medium for understanding because some studies of CLNB do address the subject of its drinking behavior and its ramifications.

Effects of Habitat Elements on Critical Biological Activities and Processes

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 potentially can significantly disrupt CLNB breeding and maternal care. However, the CEM proposes that the effects of anthropogenic disturbance on breeding and maternal care in CLNB are not well documented and therefore warrant ratings of low for understanding.
- The composition and abundance of the arthropod community across the landscape within foraging distance of CLNB daytime roosting sites strongly affects where they forage and their rate of foraging success there. However, the proposed relationship has not been studied in the Lower Colorado River Valley or elsewhere and therefore warrants ratings of low for understanding.
- Cave and cave analog distributions and their structural and thermal characteristics strongly affect site selection and roosting success for both cold- and warm-season roosting. The CEM proposes that both of these effects are well documented and well understood in the literature.

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- Interior temperatures in caves and cave analogs also strongly affect roosting site selection and roosting success for interim roosting and for both cold- and warm-season roosting. The CEM proposes that both of these effects are well documented and well understood in the literature.
- The composition and spatial structure of the tree and shrub vegetation directly affect CLNB foraging and inter-site movement, as well as predation on CLNB, with proposed high magnitude. When alternative types of tree and shrub vegetation are available within foraging distance of their roosting sites, CLNB show some selectivity in the types in which they forage. CLNB are also thought to abandon areas when suitable foraging habitat is removed (e.g., developed) within the foraging radius of the available roosting sites. And different types of tree and shrub vegetation, including around the entrances to roosting sites, produce different degrees of clutter affecting echolocation and visual scanning, which could affect CLNB abilities to detect predators. 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 CLNB 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 eight 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 CLNB adult life stage proposes the following:

- Anthropogenic disturbance may disrupt CLNB cold- and warm-season roosting and cause the bats mechanical stress, all with proposed medium magnitude, and disrupt CLNB interim roosting with low magnitude, all with low understanding. Anthropogenic disturbance also may disrupt CLNB foraging, with proposed low magnitude and low understanding.
- The arthropod community may affect both cold- and warm-season roosting site selection. CLNB adults are proposed to ignore or move away from potential daytime roosting sites when the arthropod community within foraging distance of a site does not meet the food requirements of the bats. The links are proposed to have medium understanding.
- Cave and cave analog characteristics may affect interim roosting behaviors and site selection with proposed medium understanding.

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- Monitoring, capture, handling may affect the rate of mechanical stress among CLNB with low magnitude and high understanding.
- Tree and shrub vegetation around the openings of caves and cave analogs may have low-magnitude effects on both cold- and warm-season roosting site selection. Again, however, these links are rated as having low understanding.
- The composition and density of the vertebrate community both across CLNB foraging habitat and in CLNB roosting habitat may affect the rates of competition CLNB experience for foraging and roosting habitat. However, bats are thought to partition their resource use highly effectively, such that both types of competition are minimal. The CEM therefore rates link magnitude as rated as low, but with low understanding, as the subject has not been studied.
- Water availability can have low-magnitude effects on drinking, chemical stress, and both cold- and warm-season roosting site selection. The CEM rates the effects on chemical stress and both cold- and warm-season roosting as having moderate understanding and the effect on drinking as having low understanding.

Finally, the CEM proposes that four critical biological activities and processes in the adult life stage reciprocally affect one habitat element: monitoring, capture, handling. CLNB adult foraging behaviors affect the ability of investigators to detect and distinguish their echolocation calls using acoustic monitoring equipment or to capture them in mist nets in different settings for the many reasons discussed in chapter 4 (see “Monitoring, Capture, Handling”). The CEM rates this link as having high magnitude and moderate understanding. CLNB cold- and warm-season roosting behaviors, including roosting site selection, also can affect the ability of investigators to observe and count CLNB as they exit and enter their roosting sites. The CEM rates these two links as having medium magnitude and moderate understanding. Finally, CLNB drinking behaviors may affect the ability of investigators to capture them in mist nets over water. The CEM rates this link as having high magnitude but low understanding.

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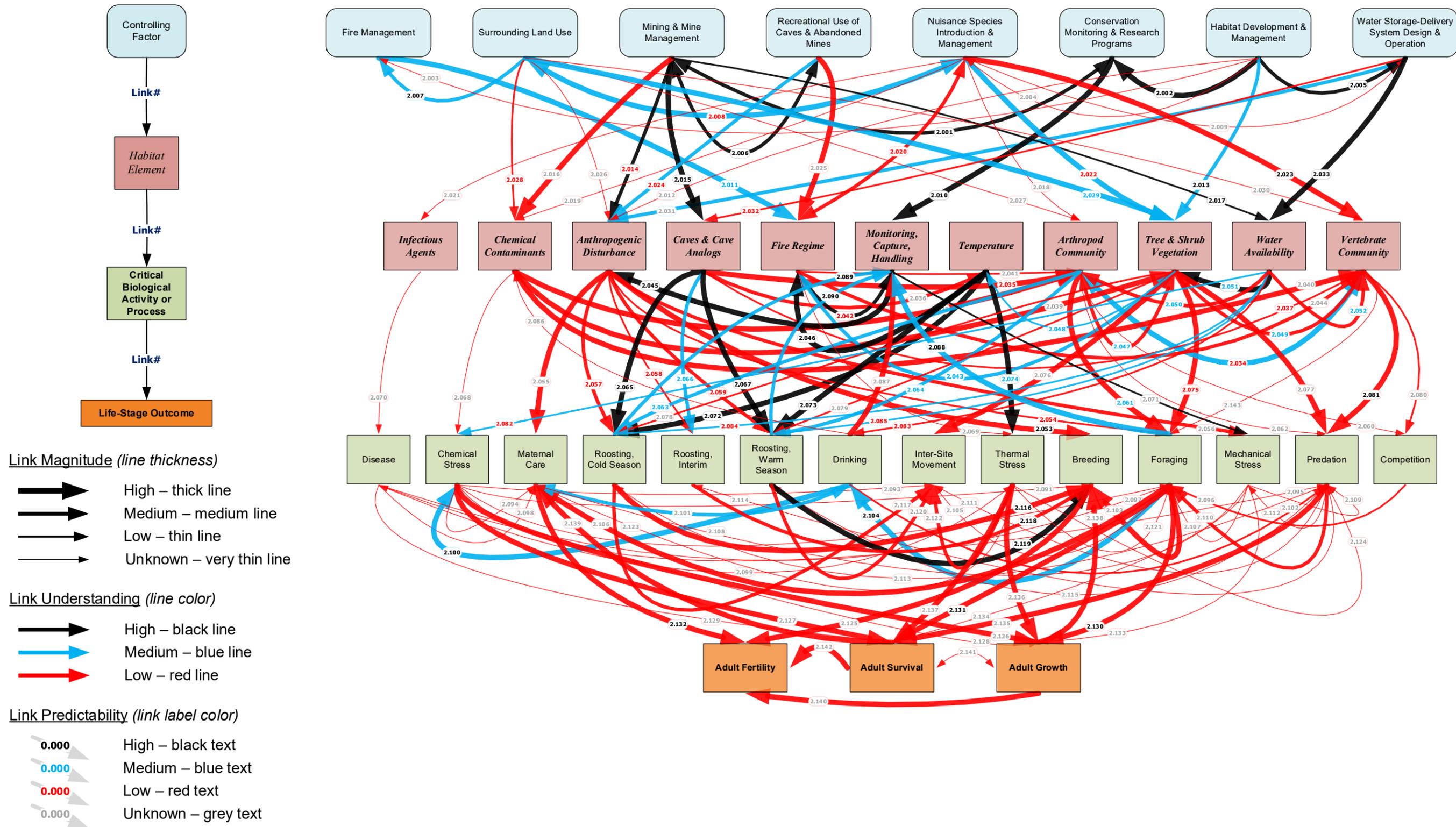


Figure 4.—CEM master diagram for CLNB life stage 2 – adult life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

Chapter 7 – Causal Relationships Across Life Stages

Chapter 6 focuses on four types of causal relationships in the CEMs for each of the three CLNB 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 the CLNB pup and adult life stages. This chapter focuses on three additional types of causal relationships across the two CLNB life stages: causal relationships (5) among habitat elements, (6) between controlling factors and habitat elements, and (7) among controlling factors. These latter three sets of relationships are essentially the same across both life stages.

This chapter discusses these last three types of causal relationships in two groups—relationships that affect CLNB 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 CLNB use as cold- and warm-season roosting (daytime 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, all presently known CLNB cold- and warm-season roosting sites lie in upland areas outside the LCR MSCP planning area. Conversely, CLNB commute from their cold- and 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.

Decades of investigations in the greater Lower Colorado River Valley and their antecedents document this broad geographic separation of activities (see publications listed in chapter 1 and older works cited therein). The distinction potentially is important to the management of habitat for CLNB. 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.

RELATIONSHIPS AFFECTING CALIFORNIA LEAF-NOSED BATS IN UPLAND HABITAT

The text and figures in chapter 6 identify six habitat elements that the CEM proposes may directly affect cold- and warm-season roosting by CLNB across the uplands surrounding the historic LCR floodplain with high, medium, low, or unknown magnitude. These habitat elements include the following:

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

In turn, four of these six 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.
- The arthropod community in caves and cave analogs and the tree and shrub vegetation around the openings to caves and cave analogs are affected by cave and cave analog characteristics and by chemical contaminants, 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.
- The arthropod community in caves and cave analogs is affected by the morphology and other characteristics of these caves and cave analogs with proposed medium magnitude and low understanding. Similarly, the arthropod community in caves and cave analogs is affected by the tree and shrub vegetation around the openings to these caves and cave analogs and by water availability in and immediately around these caves and cave analogs, also 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.

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- The arthropod community in caves and cave analogs is affected by the fire regime in these geological features, with proposed low magnitude and low understanding.

The full list of habitat elements this CEM proposes to directly or indirectly (at one remove) affect CLNB cold- and warm-season roosting therefore consists of the following nine habitat elements: anthropogenic disturbance; arthropod community (in and immediately around the entrances to caves and cave analogs); caves and cave analogs; chemical contaminants; fire regime (in and immediately around the entrances to caves and cave analogs); monitoring, capture, handling; temperature; tree and shrub vegetation (immediately around the entrances to caves and cave analogs); and water availability (in and immediately around the entrances to caves and cave analogs).

This CEM further proposes that these nine habitat elements, in turn, are shaped by six of the eight controlling factors included in the CEM. Specifically, it proposes the following:

- Conservation monitoring and research programs shape the monitoring, capture, and handling of CLNB 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.
- Water storage-delivery system design and operation affects water availability in the immediate vicinity of caves and mines in the uplands, wherever LCR impoundments have inundated or brought surface water close to caves and mines, 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, and recreational use of caves and abandoned underground mines affects the fire regime in these settings, both with proposed high magnitude but low understanding.

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- Mining and mine management shapes the frequency and severity of anthropogenic disturbance at cold- and warm-season roosting sites, with proposed medium magnitude and high understanding.
- Recreational use of caves and abandoned mines, and water storage-delivery system design and operation both shape the frequency and severity of anthropogenic disturbance at cold- and warm-season roosting sites, with proposed medium magnitude and medium understanding. The latter causal agent affects anthropogenic disturbance because the pool elevations of the LCR impoundments create boat landing sites along their shores, from which recreational explorers can more easily reach several abandoned mines.
- 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, and water storage-delivery system design and operation affects the geographic distribution of caves and cave analogs, both with proposed low magnitude and low understanding. The latter causal relationship occurs because the filling of impoundments along the LCR inundated several historic CLNB daytime roosting sites, and changes in pool elevations possibly could expose these historic sites or inundate others.
- 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 community 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. Habitat development and management by agencies with responsibilities for the lands in which CLNB cold- and warm-season roosting sites are located potentially could affect the incidence of anthropogenic disturbance at these roosting sites, also with unknown magnitude and low understanding.

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Finally, the CEM proposes that five 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.

RELATIONSHIPS AFFECTING CALIFORNIA LEAF-NOSED BATS IN LOWLAND HABITAT

Similarly, the text and figures in chapter 6 identify nine habitat elements that may particularly affect foraging (including commuting to and from foraging habitat), night roosting (interim roosting), and other critical biological activities or processes for CLNB that take place within and immediately around the historic LCR floodplain, with proposed high, medium, low, or unknown magnitude. These nine habitat elements are:

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

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- 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.
- Temperature, with proposed high-magnitude effects on thermal stress.
- The tree and shrub vegetation across this landscape, with proposed high-magnitude effects on foraging and predation.
- The vertebrate community across this landscape, with proposed high-magnitude effects on predation, low-magnitude effects on competition, and unknown-magnitude effects on foraging.
- Water availability across this landscape, with proposed low-magnitude effects on chemical stress and drinking.

In turn, these nine 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 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, tree and shrub vegetation, and vertebrate community are all potentially affected by chemical contaminants, with proposed high magnitude and low understanding.
- The arthropod community in cave analogs the bats use for interim (night) roosting is affected by characteristics of these features, with proposed high magnitude but low understanding.
- The air temperature in night roosting sites is affected by the structure and geology of the caves and cave analogs that CLNB use as night roosting sites, with proposed medium magnitude and low understanding.

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- The tree and shrub vegetation and the local fire regime across this landscape affect each, other with proposed medium magnitude and medium understanding.
- The vertebrate community is affected by the local fire regime, tree and shrub vegetation, and water availability, all with proposed medium magnitude and low understanding.
- The vertebrate community using cave analogs the bats also use for interim (night) roosting is affected by characteristics of these features, with proposed medium magnitude and low understanding.
- The arthropod community and tree and shrub vegetation affect each other, with proposed medium magnitude and low understanding.
- The arthropod community is affected by water availability, with proposed medium magnitude and low understanding.
- The arthropod community across this landscape is affected by the local fire regime, with proposed low magnitude and low understanding.
- The air temperature in night roosting sites is affected by the tree and shrub vegetation that grows around the opening to the cave or cave analog, with proposed low magnitude and medium understanding.
- The vertebrate community in cave analogs the bats use for interim (night) roosting is affected by characteristics of these features, with proposed low magnitude but low understanding.
- The vertebrate community and the tree and shrub vegetation affect each other, with proposed low magnitude and low understanding.

The full list of habitat elements that the CEM proposes to directly or indirectly (at one remove) affect foraging, commuting, night-roosting (interim roosting), and other critical biological activities or processes for CLNB within and immediately around the historic LCR floodplain therefore consists of the following 10 habitat elements: anthropogenic disturbance; arthropod community; caves and cave analogs; chemical contaminants; fire regime; monitoring, capture, handling; temperature; tree and shrub vegetation; vertebrate community; and water availability.

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

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- Conservation monitoring and research programs shape the monitoring, capture, and handling of CLNB within and immediately around the historic LCR floodplain, with proposed high magnitude and high understanding.
- Mining and mine management may shape the characteristics of caves and cave analogs used as night roosting sites in this lowland landscape by CLNB, with proposed high magnitude and high understanding.
- Water storage-delivery system design and operation shape water availability across this lowland landscape, with proposed high magnitude and high understanding.
- Fire management shapes the fire regime across this lowland landscape, and nuisance species introduction and management and surrounding land use both shape the tree and shrub vegetation in this landscape, with proposed high magnitude and medium understanding.
- Nuisance species introduction and management shapes the tree and shrub vegetation across this lowland landscape, with proposed high magnitude and medium understanding.
- Surrounding land use affects the tree and shrub vegetation across this lowland landscape, with proposed high magnitude and medium understanding.
- Mining and mine management may shape the presence and types of chemical contaminants in and around caves and cave analogs used as night roosting sites by CLNB in this lowland landscape, with proposed high magnitude and low understanding.
- Nuisance species introduction and management shapes the vertebrate community across this lowland landscape with proposed high magnitude and low understanding.
- Recreational use of caves and abandoned mines shapes the fire regime in and around caves and cave analogs used as night roosting sites by CLNB in this lowland landscape, with proposed high magnitude and low understanding.
- Habitat development and management shapes the tree and shrub vegetation across this lowland landscape, with proposed medium magnitude and medium understanding.

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- Mining and mine management, recreational use of caves and abandoned mines, and water storage-delivery system design and operation may shape the incidence and severity of anthropogenic disturbance in caves and cave analogs used as night roosting sites by CLNB, with proposed medium magnitude and high understanding. The last of these three links specifically pertains to mines accessible from the shorelines of the LCR and its impoundments.
- Nuisance species introduction and management and the local fire regime shape each other across this lowland landscape, with proposed medium magnitude and low understanding.
- Water storage-delivery system design and operation may shape the distribution of caves and cave analogs used as night roosting sites by CLNB, with proposed low magnitude and low understanding. This link specifically pertains to mines that have been or potentially could be inundated by the lake pools along the LCR.
- Surrounding land use affects the presence and concentrations of chemical contaminants to which CLNB may become exposed across this lowland landscape, with proposed low magnitude and low understanding.
- Habitat development and management shapes the incidence of anthropogenic disturbance of CLNB foraging across this lowland landscape, with proposed unknown magnitude and low understanding.
- Nuisance species introduction and management shapes the arthropod community and chemical contaminants across this lowland landscape, with proposed unknown magnitude and low understanding.
- Surrounding land use affects the incidence of anthropogenic disturbance to foraging CLNB, the arthropod community, and the vertebrate community across this lowland landscape, with proposed unknown magnitude and low understanding.

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

- Habitat development and management programs affect conservation monitoring and research programs, with proposed high magnitude and high understanding.

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- Surrounding land use and nuisance species introduction and management efforts affect each other, with proposed high magnitude and medium understanding.
- Conservation monitoring and research programs and mining and mine management—specifically, decisions on mine gating and closures—affect each other with proposed medium magnitude and high understanding.
- Habitat development and management programs affect water storage-delivery system design and operation—specifically, through calls on the system for water deliveries to habitat creation areas—with proposed medium magnitude and high understanding.
- Recreational use of caves and abandoned mines and mining and mine management—specifically, decisions on mine gating and closures—affect each other with proposed medium magnitude and high understanding.
- Surrounding land use affects the fire regime, with proposed medium magnitude and medium understanding.
- Habitat development and management programs affect fire management and nuisance species introduction and management, both with proposed unknown magnitude and low understanding.
- Water storage-delivery system design and operation and nuisance species introduction and management affect each other, with proposed unknown magnitude and low understanding.

Chapter 8 – Discussion and Conclusions

The proposed CEM for CLNB has several notable features. This chapter identifies and discusses these notable features.

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

Table 5.—Proposed magnitudes of causal relationships in CEM for the CLNB 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	8		6	18
Controlling factor	Habitat element	16	10	6	11	43
Habitat element	Habitat element	15	14	9	2	40
Habitat element	Activity or process	18	7	12	12	49
Activity or process	Habitat element	2	2	0	1	5
Activity or process	Activity or process	6	6	3	25	40
Activity or process	Life-stage outcome	15	0	1	10	26
Life-stage outcome	Activity or process	2	0	0	0	2
Life-stage outcome	Life-stage outcome	2	0	0	2	4
Column total		80	47	31	69	227

Table 6.—Proposed level of understanding of causal relationships in CEM for the CLNB 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	8	4	6	18
Controlling factor	Habitat element	9	10	24	43
Habitat element	Habitat element	6	6	28	40
Habitat element	Activity or process	8	9	32	49
Activity or process	Habitat element	0	3	2	5
Activity or process	Activity or process	1	3	36	40
Activity or process	Life-stage outcome	0	0	26	26
Life-stage outcome	Activity or process	0	0	2	2
Life-stage outcome	Life-stage outcome	0	0	4	4
Column total		32	35	160	227

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Table 5 shows that 30% (69 of 227) of all proposed causal links in the CEM, across both life stages combined, 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 CLNB 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 critical biological activities or processes (46 of 71), than of the links involving effects of life-stage outcomes (2 of 6), habitat elements (14 of 89), or controlling factors (17 of 61). This pattern reflects a lack of either anecdotes or formally collected evidence on several aspects of CLNB biology and behavior that could help guide species or habitat management.

Table 6, in turn, shows that more than 70% (160 of 227) of all proposed links in the CEM, across both life stages combined, were rated as having low understanding. Further, it is important to note that all 69 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 nearly 58% (91 of 158) 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 more strongly indicates a lack of either anecdotes or formally collected evidence on many aspects of CLNB ecology or biology or behavior that could help guide 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 the level of link understanding:

- The CEM proposes that seven controlling factors have direct, high-magnitude effects on one or more habitat elements. The controlling factors are as follows, 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—mostly concern only the uplands where CLNB in the greater LCR ecosystem seek cold- and warm-season roosts outside the LCR MSCP planning area. However, a few mines lie within the planning area. 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 low understanding to several (6 of 16) of these high-magnitude effects of controlling factors on habitat elements. Chapters 4 and 5 discuss the sources of uncertainty for these causal relationships.

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- 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. The seven habitat elements are as follows, in alphabetical order: anthropogenic disturbance, the 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 fewer than half (8 of 18) of these high-magnitude effects of habitat elements on critical biological activities and processes. One of these seven, maternal care (a habitat element for pups but a critical biological activity or process for adult females), is relevant to only to the uplands where CLNB in the greater LCR ecosystem find most of their cold- and warm-season roosts. The other six 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. The six habitat elements are as follows, in alphabetical order: anthropogenic disturbance; caves and cave analogs; chemical contaminants; monitoring, capture, handling; temperature; and water availability. Three habitat elements thus have high-magnitude *direct and indirect* effects on one or more critical biological activities or processes across the two life stages: arthropod community; caves and cave analogs; and temperature. The CEM assigns a rating of medium and low understanding to most (10 of 15) of the high-magnitude effects of habitat elements on other habitat elements. The five high-magnitude links between habitat elements with proposed ratings of high understanding are between monitoring and anthropogenic disturbance (directly affects both pup and adult life stages), between air temperature and the fire regime (directly affects both pup and adult life stages), and between water availability and the tree and shrub vegetation within the LCR planning area (directly affects only the adult life stage). Chapter 4 discusses the sources of uncertainty for these causal relationships.
- The CEM proposes that four critical biological activities and processes in the adult life stage reciprocally affect one habitat element—monitoring, capture, handling—with medium to high magnitude. (1) CLNB adult foraging behaviors constrain the ability of investigators to detect and distinguish their echolocation calls using acoustic monitoring equipment or to capture them in mist nets in different settings, for several reasons discussed in chapter 4 (see “Monitoring, Capture, Handling”). The CEM rates this link as having high magnitude and moderate understanding.

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(2) CLNB cold- and warm-season roosting behaviors, including roosting site selection, also can constrain the ability of investigators to observe and count CLNB as they exit and enter their roosting sites. The CEM rates these two links as having medium magnitude and moderate understanding. (3) CLNB drinking behaviors appear to limit the ability of investigators to capture them in mist nets over water. The CEM rates this link as having high magnitude but low understanding. The CEM thus indicates that a combination of CLNB behaviors and abilities may limit the ability of investigators to determine where and how often the bats forage, and how they behave while foraging, particularly how they orient themselves to and patrol in and around vegetation patches and openings, and how many CLNB use different foraging areas and daytime roosting sites. Another monitoring method, the tracking of individual CLNB using radio tags, has provided useful information on overall foraging ranges and routes. However, such tracking has involved only a small number of individuals and does not provide a high level of detail for studying behaviors in and around individual foraging areas.

- The CEM proposes that seven critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes across the two life stages. These seven critical biological activities or processes are as follows, in alphabetical order: breeding, with proposed high-magnitude effects on adult fertility; chemical stress, with proposed high-magnitude effects on both pup and adult growth and survival; feeding, with proposed high-magnitude effects on pup growth and survival; foraging, with proposed high-magnitude effects on adult growth and survival; maternal care, with proposed high-magnitude effects on adult fertility; predation, with proposed high-magnitude effects on adult survival; and thermal stress, with proposed high-magnitude effects on both pup and adult growth and 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 seven—breeding, feeding, and maternal care—take place exclusively in the uplands where CLNB in the greater LCR ecosystem seek cold- and warm-season roosts. Three of the other four—chemical stress, predation, and thermal stress—are proposed to affect CLNB in both the uplands and lowlands of the Lower Colorado River Valley. Only one of the seven, foraging, appears to take place mostly across the lowlands comprising the historic LCR floodplain and its immediate vicinity. Chapter 3 discusses the sources of uncertainty for these causal relationships.
- The CEM proposes that four critical biological activities or processes have direct, high-magnitude effects on one or more other critical biological activities or processes. These four thereby have (or additionally have) strong indirect effects on one or more life-stage outcomes across the two CLNB life stages. These four critical biological activities or processes are

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as follows, in alphabetical order: drinking, with proposed high-magnitude effects on chemical stress; foraging, with proposed high-magnitude effects on breeding, drinking, maternal care; and both cold- and warm-season roosting, with proposed high-magnitude effects on breeding. The CEM assigns a rating of high understanding to the relationship between warm-season roosting and breeding, ratings of medium understanding to the relationships between drinking and chemical stress and between foraging and drinking, and ratings of low understanding to the relationships between foraging and both breeding and maternal care, and between cold-season roosting and breeding. 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.

LITERATURE CITED

- Anderson, S. 1969. *Macrotus waterhousii*. American Society of Mammalogists: Mammalian Species:1–4.
- Anderson, B.W. 2012. Four Decades of Research on the Lower Colorado River. AVVAR Books, Bulletin of the Revegetation and Wildlife Management Center Volume 5, Number 1, Blythe, California.
- Andersen, D.C. and S.M. Nelson. 2013. Floral ecology and insect visitation in riparian *Tamarix* sp. (saltcedar). Journal of Arid Environments 94:105–112.
- Arizona Game and Fish Department (AZGFD). 2014. Arizona Game and Fish Department, Heritage Data Management System, Animal Abstract, *Macrotus californicus*. Unpublished abstract compiled and edited by the Heritage Data Management System. Arizona Game and Fish Department, Phoenix, Arizona.
- _____. 2019. Arizona Game and Fish Department, Heritage Data Management System, Animal Distribution Map, *Macrotus californicus*. Unpublished current distribution map dated June 12, 2019, compiled and edited by the Heritage Data Management System, Arizona Game and Fish Department, Phoenix, Arizona.
- Arizona-Sonora Desert Museum. 2019. California Leaf-nosed bat Fact Sheet. https://www.desertmuseum.org/kids/bats/california_leaf_nosed_bat.php
- AZGFD (see Arizona Game and Fish Department).
- Barclay, R.M.R. and L.D. Harder. 2003. Life histories of bats: life in the slow lane. Pages 209–253 in T.H. Kunz and M.B. Fenton (editors). Bat Ecology. University of Chicago Press, Chicago, Illinois.
- Bat World Sanctuary. 2010. Bat World Sanctuary Position Statement on Banding Insectivorous Bats. Bat World Sanctuary, Inc., Weatherford, Texas. https://batworld.org/wp-content/uploads/2011/02/BWSposition_statement-banding1.pdf
- Bean, D. and T. Dudley. 2018. A synoptic review of *Tamarix* biocontrol in North America: tracking success in the midst of controversy. BioControl:1–16.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Bell, G.P., G.A. Bartholomew, and K.A. Nagy. 1986. The role of energetics, water, economy, foraging behavior, and geothermal refugia in the distribution of the bat, *Macrotus californicus*. *Journal of Comparative Physiology B* 156:441–450.
- Berry, R., P. Brown, W. Rainey, and S. Broderick. 2017. Acoustic Monitoring for Lower Colorado River Bat Species, September 2002 to May 2007. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Blakey, R.V., R.T. Kingsford, B.S. Law, and J. Stoklosa. 2017. Floodplain habitat is disproportionately important for bats in a large river basin. *Biological Conservation* 215:1–10.
- Bradshaw, G.V.R. and A. Ross. 1961. Ectoparasites of Arizona bats. *Journal of the Arizona Academy of Science* 1:109–112.
- Braun, D.P. and R. Unnasch. 2020a. 2019 Updates to Western Red Bat (*Lasiurus blossevillii*) (WRBA) Basic Conceptual Ecological Model for the Lower Colorado River. Submitted to the Lower Colorado Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2020b. 2019 Updates to Western Yellow Bat (*Lasiurus xanthinus*) (WYBA) Basic Conceptual Ecological Model for the Lower Colorado River. Submitted to the Lower Colorado Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2020c. 2019 Townsend’s Big-eared Bat (*Corynorhinus townsendii*) (PTBB) Basic Conceptual Ecological Model for the Lower Colorado River. Submitted to the Lower Colorado Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Brennan, T.C. 2008. Online Field Guide to the Reptiles and Amphibians of Arizona.
<http://www.reptilesfaz.org/>
- Broderick, S. 2010. Post-Development Bat Monitoring, 2008 Acoustic Surveys. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2012a. Post Development Bat Monitoring, 2007–2010 Intensive Acoustic Surveys – Completion Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- _____. 2012b. Post-Development Bat Monitoring, 2009 Acoustic Surveys. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2013. Post-Development Bat Monitoring of Habitat Creation Areas Along the Lower Colorado River – 2011 Acoustic Surveys. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2014. Post Development Bat Monitoring – 2013 Acoustic Monitoring Results. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2014.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. 2016. Post-Development Acoustic Bat Monitoring 2012 – 2014 Results. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Brown, P.E. 2006. Lower Colorado River Bat Monitoring Protocol. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2010. Roost Surveys and Monitoring for Lower Colorado River Bat Species. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2013. Roost Surveys and Monitoring for Lower Colorado River Bat Species, 2013 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2015. Monitoring Colorado River Mine-Roosting Bats and Determining Their Foraging Ranges. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2015.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. *In press*. Roost Surveys and Monitoring for Lower Colorado River Bat Species, 2002–2016 Final Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Brown, P. and W. Rainey. 2016. Determining the Foraging Ranges of the California Leaf-nosed Bats Along the LCR. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2015.
<https://www.lcrmscp.gov/crtr/crtr.html>

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Bunkley, J.P., C.J.W. McClure, N.J. Kleist, C.D. Francis, and J.R. Barber. 2015. Anthropogenic noise alters bat activity levels and echolocation calls. *Global Ecology and Conservation* 3:62–71.
- Burke, M., K. Jorde, and J.M. Buffington. 2009. Application of a hierarchical framework for assessing environmental impacts of dam operation: changes in streamflow, bed mobility and recruitment of riparian trees in a western North American river. *Journal of Environmental Management* 90:S224–S236.
- Busch, D.E. 1995. Effects of fire on southwestern riparian plant community structure. *The Southwestern Naturalist* 40(3):259–267.
- Byrne, A.W., J. O’Keeffe, U. Fogarty, P. Rooney, and S.W. Martin. 2015. Monitoring trap-related injury status during large-scale wildlife management programmes: an adaptive management approach. *European Journal of Wildlife Research* 61:445–455.
- Calvert, A. 2009. 2007 Preliminary Results for the Capture of Bats at Riparian Habitat Creation Sites Along the Lower Colorado River. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2010a. Post-Development Bat Monitoring of Habitat Creation Areas along the Lower Colorado River – 2008 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2010b. Post-Development Bat Monitoring of Habitat Creation Areas Along the Lower Colorado River – 2009 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2012a. Post-Development Bat Monitoring of Habitat Creation Areas Along the Lower Colorado River – 2011 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2012b. Post-Development Bat Monitoring of Habitat Creation Areas Along the Lower Colorado River – 2010 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- _____. 2013. Post-Development Bat Monitoring of Habitat Creation Areas along the Lower Colorado River – 2012 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2014. 2013 Mist-Netting Surveys at Habitat Creation Areas. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2014.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. 2015. Eight Years of Bat Capture Surveys at Riparian Restoration Areas. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2015.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. 2016a. Post-Development Bat Monitoring of Conservation Areas and the ‘Ahakhav Tribal Preserve Along the Lower Colorado River – 2013–2014 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2016b. Post-Development Bat Monitoring of Conservation Areas and the ‘Ahakhav Tribal Preserve Along the Lower Colorado River – 2015 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2016c. Bat Monitoring at Riparian Habitat Creation Areas. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2016.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. 2017. LCR MSCP Bat Research and Monitoring: Where Did We Start, Where Are We Now? Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2017.
<https://www.lcrmscp.gov/crtr/crtr.html>
- Cockrum, E.L., B. Musgrove and Y. Petryszyn. 1996. Bats of Mojave County, Arizona. Occasional Papers – The Museum, Texas Tech University Number 157:1–71.
- Constantine, D.G. 1979. An updated list of rabies-infected bats in North America. *Journal of Wildlife Diseases* 15(2):347–349.
- Conway, C.J., C.P. Nadeau, and L. Piest. 2010. Fire helps restore natural disturbance regime to benefit rare and endangered marsh birds endemic to the Colorado River. *Ecological Applications* 20:2024–2035.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Cotten, T. and D. Grandmaison. 2013. Lowland Leopard Frog and Colorado River Toad Distribution and Habitat Use in the Greater Lower Colorado River Ecosystem, 2012 Annual Report. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Crichton, E.G. and P.H. Krutzsch (editors). 2000. Reproductive Biology of Bats. Academic Press, San Diego, California.
- Cruz-Neto, A.P., T. Garland, and A.S. Abe. 2001. Diet, phylogeny, and basal metabolic rate in phyllostomid bats. *Zoology* 104:49–58.
- Diamond, J.M. 2012. Distribution and Roost Site Habitat Requirements of Western Yellow (*Lasiurus xanthinus*) and Western Red (*Lasiurus blossevillii*) Bats: 2011 Summary Findings. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Diamond, J.M., R.J. Mixan, and M.D. Piorkowski. 2013. Distribution and Roost Site Habitat Requirements of Western Yellow (*Lasiurus xanthinus*) and Western Red (*Lasiurus blossevillii*) Bats, 2012 Summary Findings. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- DiGennaro, B., D. Reed, C. Swanson, L. Hastings, Z. Hymanson, M. Healey, S. Siegel, S. Cantrell, and B. Herbold. 2012. Using conceptual models and decision-support tools to guide ecosystem restoration planning and adaptive management: an example from the Sacramento–San Joaquin Delta, California. *San Francisco Estuary and Watershed Science* 10(3):1–15.
<http://escholarship.org/uc/item/3j95x7vt>
- Dudek. 2015. California Leaf-Nosed Bat (*Macrotus californicus*). Desert Renewable Energy Conservation Plan Proposed Land Use Plan Amendment and Final Environmental Impact Statement, Appendix Q. Bureau of Land Management in Partnership with the U.S. Fish and Wildlife Service California Energy Commission and the California Department of Fish and Wildlife, BLM/CA/PL-2016/03+1793+8321, Sacramento, California.
<http://www.drecp.org/>
- Eckberg, J.R. 2011. Las Vegas Wash Invertebrate Inventory, 2000–2010. Las Vegas Wash Coordination Committee, Las Vegas, Nevada.
- _____. 2012. Las Vegas Wash Invertebrate Inventory, 2000–2011. Las Vegas Wash Coordination Committee, Las Vegas, Nevada.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Elliott, W.R., J.R. Reddell, D.C. Rudolph, G.O. Graening, T.S. Briggs, D. Ubick, R.L. Aalbu, J. Krejca, and S.J. Taylor. 2017. The Cave Fauna of California. Proceeding of the California Academy of Sciences, Fourth Series 64.
- Ellison, L.E., T.J. O’Shea, D.J. Neubaum, M.A. Neubaum, R.D. Pearce, and R.A. Bowen. 2007. A comparison of conventional capture versus PIT reader techniques for estimating survival and capture probabilities of big brown bats (*Eptesicus fuscus*). *Acta Chiropterologica* 9:149–160.
- Ellison, L.E., E.W. Valdez, P.M. Cryan, T.J. O’Shea, and M.A. Bogan. 2013. Standard Operating Procedure for the Study of Bats in the Field. FORT IACUC SOP#: 2013-01 (Revision 2). U.S. Geological Survey, Fort Collins Science Center, Institutional Animal Care and Use Committee, Fort Collins, Colorado.
- Esbérard, C.E. and D. Vrcibradic. 2007. Snakes preying on bats: new records from Brazil and a review of recorded cases in the Neotropical region. *Revista Brasileira de Zoologia* 24(3):848–853.
- Fischenich, J.C. 2008. The application of conceptual models to ecosystem restoration. Technical Note ERDC/EBA TN-08-1. U.S. Army Corps of Engineers, Engineer Research and Development Center (ERDC), Ecosystem Management and Restoration Research Program (EMRRP), Vicksburg, Mississippi. February 2008
- Greenhall, A.M. and J.L. Paradiso. 1968. Bats and Bat Banding. Resource Publication 72:1–47. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Washington, D.C.
- Grinnell, J. 1914. An account of the mammals and birds of the Lower Colorado Valley with especial reference to the distributional problems presented. University of California Publications in Zoology 12:51–294.
- Gruver, J.C. and D.A. Keinath. 2006. Townsend’s Big-eared Bat (*Corynorhinus townsendii*): A Technical Conservation Assessment. Report prepared for the USDA Forest Service, Rocky Mountain Region, Species Conservation Project, Lakewood, Colorado.
- Hagen, E.M. and J.L. Sabo. 2012. Influence of river drying and insect availability on bat activity along the San Pedro River, Arizona (USA). *Journal of Arid Environments* 84:1–8.
- _____. 2014. Temporal variability in insectivorous bat activity along two desert streams with contrasting patterns of prey availability. *Journal of Arid Environments* 102:104–112.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Hammerson, G.A., M. Kling, M. Harkness, M. Ormes, and B.E. Young. 2017. Strong geographic and temporal patterns in conservation status of North American bats. *Biological Conservation* 212:144–152.
- Hautzinger, A. 2010. Ecological Flows on the Bill Williams River. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2010.
<https://www.lcrmscp.gov/crtr/crtr.html>
- Hernández-Jerez, A., P. Adriaanse, A. Aldrich, P. Berny, T. Coja, S. Duquesne, A. L. Gimsing, M. Marina, M. Millet, O. Pelkonen, S. Pieper, A. Tiktak, I. Tzoulaki, A. Widenfalk, G. Wolterink, D. Russo, F. Streissl, and C. Topping. 2019. Scientific statement on the coverage of bats by the current pesticide risk assessment for birds and mammals. *EFSA Journal* 17(7):5758.
- Hill, J. 2011. Genetic Characterization of *Macrotus californicus* Populations Along the Lower Colorado River, 2010 Annual Report. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2016. Genetic Characterization of the California Leaf-nosed Bat (*Macrotus californicus*) Along the Lower Colorado River. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2018. Post-Development Bat Monitoring of Conservation Areas and the ‘Ahakhav Tribal Preserve Along the Lower Colorado River – 2013–2014 Capture Surveys. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2019a. Genetic Characterization of the California Leaf-nosed Bat (*Macrotus californicus*) Along the Lower Colorado River, Final Report. Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2019b. Jeff Hill, Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada, personal communication. September 2019.
- _____. 2020. Jeff Hill, Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada, personal communication. February 2020.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Hill, J. and C. Ronning. 2018. Jeff Hill and Carrie Ronning, Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada, joint personal communication. February 2018.
- Huey, L.M. 1925. Food of the California leaf-nosed bat. *Journal of Mammalogy* 6:196–197.
- Jacobson, R.B., M.L. Annis, M.E. Colvin, D.A. James, T.L. Welker, and M.J. Parsley. 2016. Missouri River *Scaphirhynchus albus* (Pallid Sturgeon) Effects Analysis—Integrative Report, 2016. Scientific Investigations Report 2016–5064. U.S. Geological Survey Reston, Virginia.
- Kauffman, J.B., R.L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22:12–24.
- Kondolf, G.M., J.G. Williams, T.C. Horner, and D. Milan. 2008. Assessing physical quality of spawning habitat. Pages 249–274 in D.A. Sear and P. DeVries (editors). *Salmonid Spawning Habitat in Rivers: Physical Controls, Biological Responses, and Approaches*. American Fisheries Society Symposium 65. American Fisheries Society, Bethesda, Maryland.
- Krueper, D.J. 1993. Effects of land use practices on western riparian ecosystems. Pages 321–330 in D.M. Finch and P.W. Stangel (editors). *Status and Management of Neotropical Migratory Birds*. Rocky Mountain Forest and Range Experiment Station GTR RM-229.
- Krueper, D.J., J. Bart, and T.D. Rich. 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona. *Conservation Biology* 17:607–615.
- Lang, A.B., E.K.V. Kalko, H. Römer, C. Bockholdt, and D.K.N. Dechmann. 2006. Activity levels of bats and katydids in relation to the lunar cycle. *Oecologia* 146:659–666.
- Lower Colorado River Multi-Species Conservation Program (LCR MSCP). 2004. Lower Colorado River Multi-Species Conservation Program, Volume II: Habitat Conservation Plan, Final. December 17 (J&S 00450.00). Sacramento, California.
- _____. 2008. Post-Development Bat Monitoring of Habitat Creation Areas Along the Lower Colorado River – 2007 Acoustic Surveys. Bureau of Reclamation, Boulder City, Nevada.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- _____. 2009. Effects of Abiotic Factors on Insect Populations in Riparian Restoration Sites, 2007 Annual Report. Bureau of Reclamation, Boulder City, Nevada.
- _____. 2014. Final Implementation Report, Fiscal Year 2015 Work Plan and Budget, Fiscal Year 2013 Accomplishment Report. Bureau of Reclamation, Boulder City, Nevada.
- _____. 2016. Species Accounts for the Lower Colorado River Multi-Species Conservation Program. Bureau of Reclamation, Boulder City, Nevada.
- _____. 2018a. Final Implementation Report, Fiscal Year 2019 Work Plan and Budget, Fiscal Year 2017 Accomplishment Report. Bureau of Reclamation, Boulder City, Nevada.
- _____. 2018b. Five-Year Monitoring and Research Priorities for the Lower Colorado Multi-Species Conservation Program, 2018–2022. Bureau of Reclamation, Boulder City, Nevada.
- Maturango Museum and Brown-Berry Biological Consulting. 2018. California Leaf-nosed and Townsend's Big-eared Bat Foraging Distance Survey, 2017. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139–185 in D.M. Power (editor). Current Ornithology. Plenum Press, New York, New York.
- Messenger, S.L., C.E. Rupprecht, and J.S. Smith. 2003. Bats, emerging virus infections, and the rabies paradigm. Pages 622–679 in T.H. Kunz and M.B. Fenton (editors). Bat Ecology. University of Chicago Press, Chicago, Illinois.
- Meyer, R. 2005. Species: *Atriplex lentiformis*. Fire Effects Information System. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Fire Sciences Laboratory, Fort Collins, Colorado.
<https://www.fs.fed.us/database/feis/plants/shrub/atrlen/all.html>
- Mikula, P. 2015. Fish and amphibians as bat predators. European Journal of Ecology 1:71–80.
- Mikula, P., F. Morelli, R.K. Lučan, D.N. Jones, and P. Tryjanowski. 2016. Bats as prey of diurnal birds: a global perspective. Mammal Review 46:160–174.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Miller, J.D. and D.J. Leavitt. 2015. Development and Implementation of a Repeatable Monitoring Plan for Lowland Leopard Frogs and Colorado River Toads on the Lower Colorado River, 2015 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Minckley, W.L. and J.N. Rinne. 1985. Large woody debris in hot-desert streams: a historical review. *Desert Plants* 7:142–153.
- Mixan, R.J. 2015. Acoustic Monitoring at Non-Restoration Sites Along the LCR. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2015.
<https://www.lcrmscp.gov/crtr/crtr.html>.
- _____. 2016. MSCP System Wide Acoustic Monitoring Along The LCR. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2016.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. 2017. MSCP Conservation Area and System Wide Acoustic Monitoring. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2017.
<https://www.lcrmscp.gov/crtr/crtr.html>
- Mixan, R.J. and J.M. Diamond. 2014a. Monitoring of LCR MSCP Bat Species as Determined by Acoustic Sampling, 2013 Summary Findings. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2014b. Temporal Occupancy of MSCP Bat Species along the LCR. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2017.
<https://www.lcrmscp.gov/crtr/crtr.html>
- _____. 2016. 2015 System-Wide Acoustic Monitoring of LCR MSCP Bat Species. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2017a. 2014 System-Wide Acoustic Monitoring of LCR MSCP Bat Species. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2017b. 2016 System-Wide Acoustic Monitoring of LCR MSCP Bat Species. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- _____. 2018a. 2017 System-Wide Acoustic Monitoring of LCR MSCP Bat Species. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2018b. Post-Development Acoustic Monitoring of LCR MSCP Bat Species, 2015 – 2016 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2019a. 2018 System-Wide Acoustic Monitoring of LCR MSCP Bat Species. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2019b. Post-Development Acoustic Monitoring of LCR MSCP Bat Species, 2017 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Mixan, R.J., J.M. Diamond, and L. Piest. 2012. Monitoring of LCR MSCP Bat Species as Determined by Acoustic Sampling – Summary Findings 2011. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Mixan, R.J., J.M. Diamond, and M. Piorkowski. 2013. Monitoring of LCR MSCP Bat Species as Determined by Acoustic Sampling, 2012 Summary Findings. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Mixan, R.J., J.M. Diamond, M.D. Piorkowski, and D.P. Sturla. 2015. Distribution and Roost Site Habitat Requirements of the Western Yellow Bat (*Lasiurus blossevillii*) and the Western Yellow Bat (*Lasiurus xanthinus*). Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Molinari, J., E.E. Gutiérrez, A.A. De Ascensão, J.M. Nassar, A. Arends, and R.J. Márquez. 2005. Predation by giant centipedes, *Scolopendra gigantea*, on three species of bats in a Venezuelan cave. *Caribbean Journal of Science* 41:340–346.
- Morgan, C.N., L.K. Ammerman, K.D. Demere, J.B. Doty, Y.J. Nakazawa, and M. R. Mauldin. 2019. Field Identification Key and Guide for Bats of the United States of America. *Occasional Papers of the Museum of Texas Tech University* 360.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Mueller, G.A. 2006. Ecology of Bonytail and Razorback Sucker and the Role of Off-Channel Habitats in Their Recovery. Scientific Investigations Report 2006-5065. U.S. Geological Survey, Reston, Virginia.
- Murphy, D.D. and P.S. Weiland. 2011. The route to best science in implementation of the Endangered Species Act's consultation mandate: the benefits of structured effects analysis. *Environmental Management* 47:161–72.
- _____. 2014. Science and structured decision making: fulfilling the promise of adaptive management for imperiled species. *Journal of Environmental Studies and Sciences* 4:200–207.
- National Park Service Institutional Animal Care and Use Committee. 2016. National Park Service Institutional Animal Care and Use Committee Standard Operating Procedure for the Study of Bats in the Field. National Park Service, Washington, D.C.
- NatureServe. 2019. Species Comprehensive Report – *Macrotus californicus*. NatureServe Explorer: An online encyclopedia of life [Web application]. Version 7.1. NatureServe, Arlington, Virginia.
<http://explorer.natureserve.org>
- Nelson, S.M. 2009. Comparison of Terrestrial Invertebrates Associated with Las Vegas Wash Exotic Vegetation and Planted Native Vegetation Sites. Technical Memorandum No. 86-68220-09-11. U.S. Department of the Interior, Bureau of Reclamation Denver, Colorado.
- Nelson, S.M. and R. Wydoski. 2013. Butterfly assemblages associated with invasive Tamarisk (*Tamarix* spp.) sites: comparisons with tamarisk control and native vegetation reference sites. *Journal of Insects* 2013:Article ID 561617.
- Nelson, S.M., R. Wydoski, and J. Keele. 2015. Monitoring MacNeill's Sootywing and its Habitats. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Nyffeler, M. and M. Knörnschild. 2013. Bat predation by spiders. *PLoS One* 8:e58120.
- O'Donnell, R.P. and D.J. Leavitt. 2017a. Development and Implementation of a Repeatable Monitoring Plan for Lowland Leopard Frogs and Colorado River Toads on the Lower Colorado River, 2016 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- _____. 2017b. Development and Implementation of a Repeatable Monitoring Plan for Lowland Leopard Frogs and Colorado River Toads on the Lower Colorado River. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- O'Farrell, M.J. 1970. Notes on the distribution of *Macrotus waterhousii* in Southern Nevada. *Great Basin Naturalist* 30:53.
- O'Shea, T.J., L.E. Ellison, and T.R. Stanley. 2004. Survival estimation in bats: historical overview, critical appraisal, and suggestions for new approaches. Pages 297–336 in W. Thompson (editor). *Sampling Rare or Elusive Species: Concepts, Designs, and Techniques for Estimating Population Parameters*. Island Press, Washington, D.C.
- O'Shea, T.J., P.M. Cryan, and M.A. Bogan (editors). 2018. United States Bat Species of Concern: a Synthesis. *Proceedings of the California Academy of Sciences (Series 4)* 65.
- Ohmart, R.D., B.W. Anderson, and W.C. Hunter. 1988. The Ecology of the Lower Colorado River from Davis Dam to the Mexico-United States International Boundary: A Community Profile. *Biological Report 85(7.19)*. U.S. Department of the Interior, U.S. Fish and Wildlife Service, Research and Development, Washington, D.C.
- Orr, T.J. and M. Zuk. 2013. Does delayed fertilization facilitate sperm competition in bats? *Behavioral Ecology and Sociobiology* 67:1903–1913.
- Pratt, G.F. and W.D. Wiesenborn. 2009. MacNeill's sootywing (*Hesperopsis graciellae*) (Lepidoptera: HesperIIDae) behaviors observed along transects. *Proceedings of the Entomological Society of Washington* 111:698–707.
- _____. 2011. Geographic distribution of MacNeill's sootywing (*Hesperopsis graciellae*) (Lepidoptera: HesperIIDae) along the lower Colorado River floodplain. *Proceedings of the Entomological Society of Washington* 113:31–41.
- Rabe, M.J. and S.S. Rosenstock. 2005. Influence of water size and type on bat captures in the lower Sonoran Desert. *Western North American Naturalist* 65:87–90.
- Randall, J.M., S.S. Parker, J. Moore, B. Cohen, L. Crane, B. Christian, D. Cameron, J. MacKenzie, K. Klausmeyer, and S. Morrison. 2010. Mojave Desert Ecoregional Assessment. The Nature Conservancy in California, San Francisco, California.

Reclamation (see Bureau of Reclamation).

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- RiversEdge West. 2019. 2007–2018 Distribution of Tamarisk Beetle (*Diorhabda* spp.). RiversEdge West, Grand Junction, Colorado.
<https://riversedgewest.org/events/tamarisk-beetle-maps>
- Ronning, C. 2020. Carolyn Ronning, Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada, personal communication. February 2020.
- Ross, A. 1964. Ecological aspects of the food habits of some insectivorous bats. Ph.D. Dissertation. University of Arizona, Zoology, Tucson, Arizona.
- Rubin, Z., B. Rios-Touma, and M. Kondolf. 2014. Insect (Prey) Availability in Restoration Sites. Presentation, Colorado River Terrestrial and Riparian (CRTR) meeting, Laughlin, Nevada. January 2014.
<https://www.lcrmsep.gov/crtr/crtr.html>
- Saldaña-Vázquez, R.A. and M.A. Munguía-Rosas. 2013. Lunar phobia in bats and its ecological correlates: a meta-analysis. *Mammalian Biology* 78:216–219.
- Shafroth, P.B., and V.B. Beauchamp. 2006. Defining Ecosystem Flow Requirements for the Bill Williams River, Arizona. Open File Report 2006-1314. U.S. Geological Survey Reston, Virginia.
- Sikes, R.S. and Animal Care and Use Committee of the American Society of Mammalogists. 2016. 2016 Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education. *Journal of Mammalogy* 97:663–688.
- Spotswood, E.N., K.R. Goodman, J. Carlisle, R.L. Cormier, D.L. Humple, J. Rousseau, S.L. Guers, and G.G. Barton. 2011. How safe is mist netting? Evaluating the risk of injury and mortality to birds. *Methods in Ecology and Evolution* 3:29–38.
- Stromberg, J. 1998. Dynamics of Fremont cottonwood (*Populus fremontii*) and saltcedar (*Tamarix chinensis*) populations along the San Pedro River, Arizona. *Journal of Arid Environments* 40:133–155.
- Stromberg, J.C., T.J. Rychener, and M.D. Dixon. 2009. Return of fire to a free-flowing desert river: effects on vegetation. *Restoration Ecology* 17:327–338.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Stuchin, M., C.M. Machalaba, K.J. Olival, M. Artois, R.G. Bengis, P. Caceres, F. Diaz, E. Erlacher-Vindel, S. Forcella, F.A. Leighton, K. Murata, M. Popovic, P. Tizzani, G. Torres, and W.B. Karesh. 2018. Rabies as a threat to wildlife. *Revue Scientifique et Technique (International Office of Epizootics)* 37:341–357.
- Tobin, A. and C.L. Chambers. 2017. Mixed effects of gating subterranean habitat on bats: a review. *Journal of Wildlife Management* 81:1149–1160.
- Trathnigg, H.K. and F.O. Phillips. 2015. Importance of native understory for bird and butterfly communities in a riparian and marsh restoration project on the lower Colorado River, Arizona. *Ecological Restoration* 33:395–407.
- Tuttle, M. D. 1998. The California leaf-nosed bat, sophisticated desert survivor. *BATS Magazine* 16:5–10.
- Tuttle, M.D. and A. Moreno. 2005. Cave-dwelling Bats of Northern Mexico: Their value and Conservation Needs. *Bat Conservation International*, Austin, Texas.
- Vizcarra, B. 2011. Evaluating Use of Habitat by Bats Along the Lower Colorado River. MS Thesis. Northern Arizona University, School of Forestry, Flagstaff, Arizona.
- Vizcarra, B. and L. Piest. 2009. Monitoring of Covered and Evaluation Bat Species for the LCR MSCP: 2008 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2010. Monitoring of Covered and Evaluation Bat Species for the Lower Colorado River Multi-Species Conservation Program — 2009 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Vizcarra, B., L. Piest, and V. Frary. 2010. Monitoring of Covered and Evaluation Bat Species for the Lower Colorado River Multi-Species Conservation Program — 2010 Final Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Voigt, C.C. and T. Kingston (editors). 2016. *Bats in the Anthropocene: Conservation of Bats in a Changing World*. Springer International Publishing, New York, New York.

**California Leaf-nosed Bat (*Macrotus californicus*) (CLNB)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Western Bat Working Group. 2019. Western Bat Working Group, Western Species Accounts, *Macrotus californicus*, California leaf-nosed bat. <http://wbwg.org/western-bat-species/>
- Wiesenborn, W.D. 2010. Effects of Abiotic Factors on Insect Populations in Riparian Restoration Sites, 2008 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2012. Effects of Abiotic Factors on Insect Populations in Riparian Restoration Sites, 2009 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2013. Effects of Abiotic Factors on Insect Populations in Riparian Restoration Sites, 2010 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2014a. Effects of Abiotic Factors on Insect Populations in Riparian Restoration Sites, 2012 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- _____. 2014b. Effects of Abiotic Factors on Insect Populations in Riparian Restoration Sites, 2011 Annual Report. Submitted to the Lower Colorado River Multi-Species Conservation Program, Bureau of Reclamation, Boulder City, Nevada.
- Wiesenborn, W.D., S.L. Heydon, and K. Lorenzen. 2008. Pollen loads on adult insects from tamarisk flowers and inferences about larval habitats at Topock Marsh, Arizona. *Journal of the Kansas Entomological Society* 81:50–60.
- Wildhaber, M.L., A.J. DeLonay, D.M. Papoulias, D.L. Galat, R.B. Jacobson, D.G. Simpkins, P.J. Baaten, C.E. Korschgen, and M.J. Mac. 2007. A conceptual life-history model for pallid and shovelnose sturgeon. Circular 1315. U.S. Geological Survey, Reston, Virginia.
- _____. 2011. Identifying structural elements needed for development of a predictive life-history model for pallid and shovelnose sturgeons. *Journal of Applied Ichthyology* 27:462–469.

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Wilkinson, G.S. and J.M. South. 2002. Life history, ecology and longevity in bats. *Aging cell* 1:124–131.

Wonkka, C.L., D. Twidwell, C.H. Bielski, C.R. Allen, and M.C. Stambaugh. 2018. Regeneration and invasion of cottonwood riparian forest following wildfire. *Restoration Ecology* 26:456–465.

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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, the 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:

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- **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

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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.

The present 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.

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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):

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- (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 present 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.

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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 (at the end of this attachment) presents the scoring framework for link predictability.

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- **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 (at the end of this attachment) 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 to 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 (at the end of this attachment). 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 (at the end of this attachment) 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 <i>at the places and times where the effect occurs</i> .	
High	Even a relatively small change in the causal node will result in a relatively large change in the affected node <i>at the places and times where the effect occurs</i> .
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 <i>at the places and times where the effect occurs</i> .
Low	Even a relatively large change in the causal node will result in only a relatively small change in the affected node <i>at the places and times where the effect occurs</i> .
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.

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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.

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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	<i>(The “Low” rank includes this condition).</i>

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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 <i>management actions and options</i> , 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 <i>basic scientific knowledge</i> , 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.

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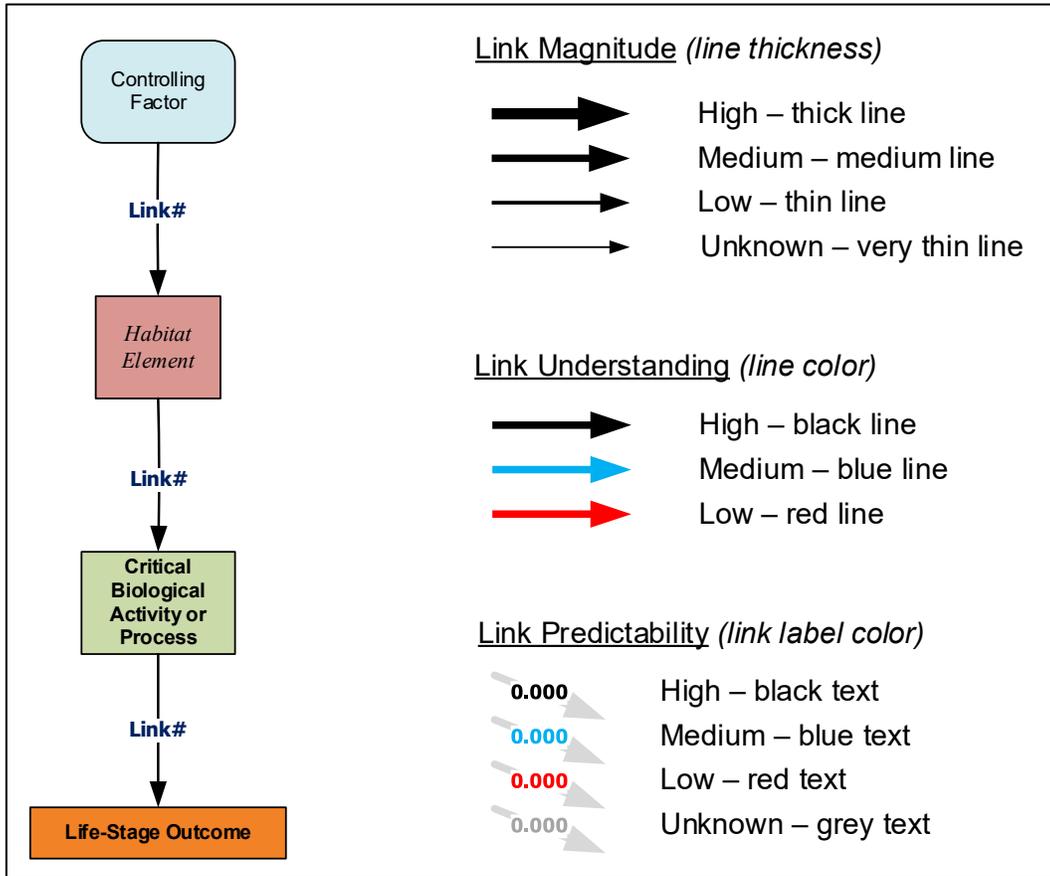


Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

LITERATURE CITED

- Burke, M., K. Jorde, and J.M. Buffington. 2009. Application of a hierarchical framework for assessing environmental impacts of dam operation: changes in streamflow, bed mobility and recruitment of riparian trees in a western North American river. *Journal of Environmental Management* 90:S224–S236.
- DiGennaro, B., D. Reed, C. Swanson, L. Hastings, Z. Hymanson, M. Healey, S. Siegel, S. Cantrell, and B. Herbold. 2012. Using conceptual models and decision-support tools to guide ecosystem restoration planning and adaptive management: an example from the Sacramento–San Joaquin Delta, California. *San Francisco Estuary and Watershed Science* 10(3):1–15.
<http://escholarship.org/uc/item/3j95x7vt>
- Fischenich, J.C. 2008. The application of conceptual models to ecosystem restoration. Technical Note ERDC/EBA TN-08-1. U.S. Army Corps of Engineers, Engineer Research and Development Center (ERDC), Ecosystem Management and Restoration Research Program (EMRRP). Vicksburg, Mississippi. February 2008
<http://el.erdc.usace.army.mil/publications.cfm?Topic=technote&Code=emrrp>
- Kondolf, G.M., J.G. Williams, T.C. Horner, and D. Milan. 2008. Assessing physical quality of spawning habitat. Pages 249–274 in D.A. Sear and P. DeVries (editors). *Salmonid Spawning Habitat in Rivers: Physical Controls, Biological Responses, and Approaches*. American Fisheries Society Symposium 65. American Fisheries Society, Bethesda, Maryland.
- McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139–185 in D.M. Power (editor). *Current Ornithology*. Plenum Press, New York, New York.
- Wildhaber, M.L., A.J. DeLonay, D.M. Papoulias, D.L. Galat, R.B. Jacobson, D.G. Simpkins, P.J. Baaten, C.E. Korschgen, and M.J. Mac. 2007. A conceptual life-history model for pallid and shovelnose sturgeon. Circular 1315. U.S. Geological Survey, Reston, Virginia.
- _____. 2011. Identifying structural elements needed for development of a predictive life-history model for pallid and shovelnose sturgeons. *Journal of Applied Ichthyology* 27:462–469.