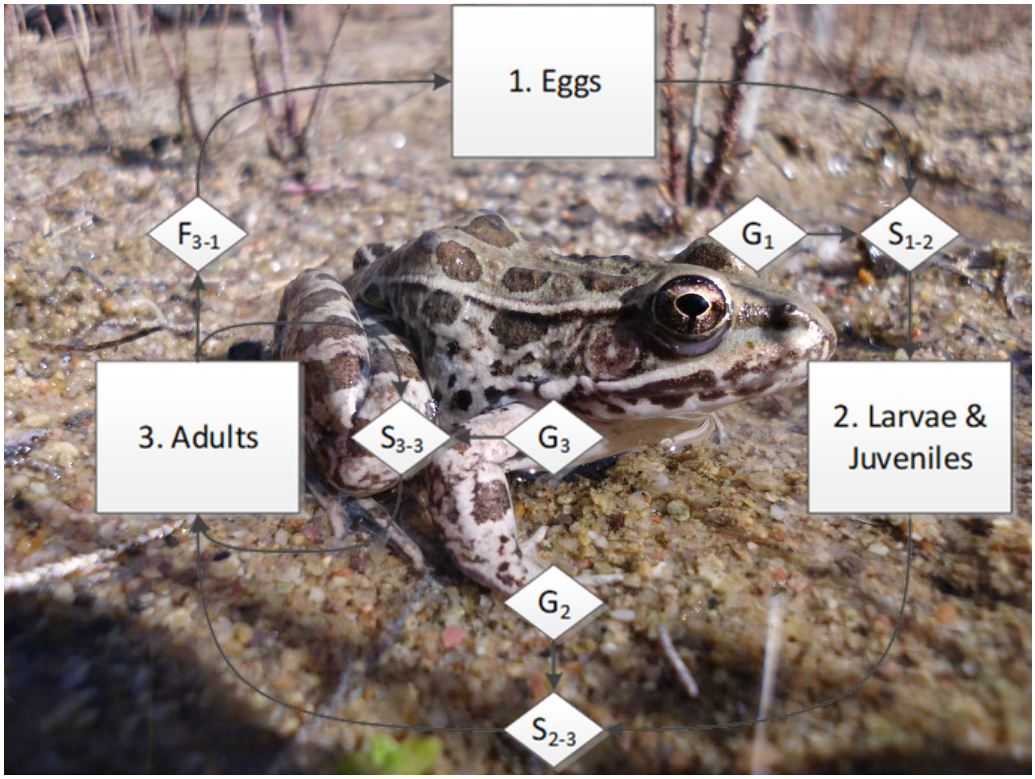
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Lowland Leopard Frog (*Rana* = *Lithobates yavapaiensis*) Basic Conceptual Ecological Model for the Lower Colorado River



Lowland leopard frog in Graham County, Arizona (Arizona Game and Fish Department).

BUREAU OF RECLAMATION

Work conducted under LCR MSCP Work Task G6

February 2020

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Lower Colorado River Multi-Species Conservation Program

Lowland Leopard Frog (*Rana = Lithobates yavapaiensis*) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

ADEQ	Arizona Department of Environmental Quality
aka	also known as
AZGFD	Arizona Game and Fish Department
Bd	*Batrachochytrium dendrobatidis*
CEM	conceptual ecological model
cm	centimeter(s)
DAR	digital automated recorder
DNA	deoxyribonucleic acid
DO	dissolved oxygen
DOC	dissolved organic carbon
eDNA	environmental deoxyribonucleic acid
EPA	Environmental Protection Agency
ERP	Sacramento-San Joaquin Delta Ecosystem Restoration Program
FTA	funnel trap array
ft^3/s	cubic feet per second
h	hour(s)
HCP	Habitat Conservation Plan
Hg(II)	mercury (+2) cation
km	kilometer(s)
L	liter(s)
LC_{50}	lethal concentration 50
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
LLFR	lowland leopard frog (*Rana* = *Lithobates yavapaiensis*)
MeHg	methyl-mercury
m	meter(s)
m^2	square meter(s)
mg	milligram(s)
mm	millimeter(s)
m^3/s	cubic meter(s) per second
mo	month
mtDNA	mitochondrial deoxyribonucleic acid

NH^3	ammonia
pH	measure of the acidity or alkalinity of a solution
POM	particulate organic matter
Reclamation	Bureau of Reclamation
SVL	snout-vent length
USDA	U.S. Department of Agriculture
USFWS	U.S. Fish and Wildlife Service
USGS	U.S. Geological Survey
UV-B radiation	ultraviolet-B radiation
VES	visual encounter survey
VES C/R	visual encounter survey with an audio broadcast call/response component

Symbols

°C	degrees Celsius
>	greater than
≥	greater than or equal to
<	less than
‰	parts per thousand
%	percent (parts per hundred)
±	plus or minus

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. 2003[1]). The model building process can be as informative as the model itself, as it reveals what is known and what is unknown about the connections and causalities in the systems under management.

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

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

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

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

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

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

How to Use the Models

There are three important elements to each CEM:

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

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

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

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

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

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

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

Executive Summary

This document presents a conceptual ecological model (CEM) for the lowland leopard frog (*Rana = Lithobates yavapaiensis*) (LLFR). The purpose of this model is to help the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Bureau of Reclamation, identify areas of scientific uncertainty concerning LLFR ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure LLFR 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 present LLFR population and its distribution within the greater lower Colorado River ecosystem in Reaches 3–7 along the Colorado River main stem and in the Bill Williams River watershed. Within the greater LCR ecosystem, LLFR currently occur only in the Bill Williams River watershed. However, LLFR occurred historically across the entire LCR floodplain along Reaches 3–7, and recent studies have identified habitat along these floodplain reaches that potentially could support LLFR. The model addresses the landscape as a whole rather than any single managed area.

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 LLFR. 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 the Bureau of Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

CONCEPTUAL ECOLOGICAL MODELS

CEMs integrate and organize existing knowledge concerning: (1) what is known about an ecological resource, with what certainty, and the sources of this information, (2) critical areas of uncertain or conflicting science that demand resolution to better guide management planning and action, (3) crucial attributes to use while monitoring system conditions and predicting the effects of experiments, management actions, and other potential agents of change, and (4) how we expect the characteristics of the resource to change as a result of altering its shaping/controlling factors, including those resulting from management actions.

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

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

- **Life stages** – These consist of the major growth stages and critical events through which an individual LLFR must pass in order to complete a full reproductive 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).

- **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.

- **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.

- **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."

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

conceptual ecological models allow users to query the CEM spreadsheet for each life stage and generate diagrams that selectively display query results concerning the CEM for each life stage.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The information used to construct the present CEM includes the most recent LCR MSCP species account (LCR MSCP 2016) and the online account by Sredl (2018), which updates information from Sredl (2005); information from the Arizona Game and Fish Department (AZGFD) Heritage Data Management System Animal Abstract for LLFR (AZGFD 2006); websites; recent journal articles; reports by the AZGFD to the LCR MSCP ((Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b); studies of LLFR in other areas (Rosen et al. 2013; Swann and Wallace 2010; Wallace et al. 2010); studies of closely related leopard frog species in the Southwestern United States, particularly the Chiricahua leopard frog (*Rana = Lithobates chiricahuensis*) (AZGFD 2015; Hinderer et al. 2017; Sredl and Jennings 2018) and relict leopard frog (*Rana = Lithobates onca*[1]) (AZGFD 2003; Goldstein et al. 2017; Jaeger et al. 2017; Oláh-Hemmings et al. 2010); general works on the types of southwestern aquatic and wetland settings in which LLFR can occur; studies and overviews of frog biology and ecology in general; and the expert knowledge of LCR MSCP biologists. However, the purpose of the present report is not to provide an updated literature review; rather, its purpose is to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

The LLFR conceptual ecological model identifies three life stages based on the aforementioned sources of information. Further, the CEM identifies two or more life-stage outcomes for each life stage as follows:

- Eggs: egg growth, egg survival
- Larvae and juveniles: larval-juvenile growth, larval-juvenile survival
- Adults: adult growth, adult survival, adult fertility, gene flow

Chapter 2 defines and discusses these life stages and life-stage outcomes in detail. The CEM includes growth as a life-stage outcome for all three life stages based

[1] Use of the "Lithobates" nomenclature to replace "Rana" is controversial (Sredl 2018). The formal designation in the present document follows AZGFD (2006) and NatureServe (2018).

on the extensive literature on frog biology indicating that the rates of growth and attained sizes in all three life stage affect survival rates, adult mating success, and fertility. The CEM includes gene flow as a life-stage outcome for the adult life stage because such flow is crucial to maintaining the overall genetic diversity of the species as a whole—a diversity potentially threatened by population fragmentation.

The LLFR conceptual ecological model identifies 12 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 12 critical biological activities and processes are as follows, in alphabetical order: chemical stress, competition, disease, foraging, hybridization, hydration stress, mating and ovipositing, mechanical stress, occupancy and inter-site movement, predation, resting/hiding, and thermal stress.

The LLFR conceptual ecological model distinguishes 15 habitat elements that affect the rates, timing, magnitude, distribution, or other aspects of 1 or more critical biological activities or processes for 1 or more life stages. Chapter 4 defines and discusses these habitat elements in detail. The 15 habitat elements are as follows, in alphabetical order: airborne contaminants; birds and mammals; drainage network connectivity; fire regime; fish and herpetofauna; herbaceous vegetation; hydrologic regime; infectious agents; macroinvertebrates; monitoring, capture, handling; periphyton and particulate organic matter (POM); substrate; water chemistry; water temperature; and woody vegetation.

Finally, the LLFR conceptual ecological model distinguishes 10 controlling factors that affect the distribution, quality, composition, abundance, and other features of 1 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 10 controlling factors are as follows, in alphabetical order: channel and off-channel engineering, conservation monitoring and research programs, fire management, fisheries management, land use, nuisance species introduction and management, onsite vegetation management, onsite water management, wastewater and other contaminant inflows, and water storage-delivery system design and operations.

RESULTS

The CEM identifies the following direct, strong (high-magnitude) causal relationships among these controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes:

- Seven controlling factors—conservation monitoring and research programs; fire management; fisheries management; land use; nuisance species introduction and management; onsite water management; and water storage-delivery system design and operations—have direct, high-magnitude effects on one or more habitat elements relevant to one or more LLFR life stages.

- Twelve habitat elements—birds and mammals; drainage network connectivity; fish and herpetofauna; herbaceous vegetation; hydrologic regime; infectious agents; macroinvertebrates; monitoring, capture, handling; periphyton and particulate organic matter (POM); substrate; water temperature; and woody vegetation—have direct, high-magnitude effects on one or more critical biological activities and processes among the three LLFR life stages.

- Nine habitat elements—birds and mammals; fire regime; fish and herpetofauna; herbaceous vegetation; hydrologic regime; macroinvertebrates; substrate; water temperature; and woody vegetation—have direct, high-magnitude effects on one or more other habitat elements. These nine habitat elements thereby have (or additionally have) strong indirect effects on one or more critical biological activities or processes in one or more life stages. Eight habitat elements in total—birds and mammals; fish and herpetofauna; herbaceous vegetation; hydrologic regime; macroinvertebrates; substrate; water temperature; and woody vegetation—have both *direct and indirect* high-magnitude effects on one or more critical biological activities or processes among the three LLFR life stages.

- Four critical biological activities or processes—foraging; mating and ovipositing; occupancy and inter-site movement; and predation—have direct, high-magnitude effects on one or more life-stage outcomes among the three LLFR life stages. Foraging specifically has direct, high-magnitude effects on larval-juvenile growth, larval-juvenile survival, and adult growth. Mating and ovipositing has direct, high-magnitude effects on adult fertility. LLFR occupancy and inter-site movement has direct, high-magnitude effects on gene flow. Predation has direct, high-magnitude effects on survival in all three life stages.

- Two critical biological activities or processes—competition and predation—have direct, high-magnitude effects on another critical biological process, occupancy and inter-site movement. Competition and predation thus have important secondary effects on gene flow.

The CEM also identifies a large number of potential causal relationships with low understanding. These include several links for which the available information indicates a likely high-magnitude but currently poorly understood relationship, and links for which the available information is too scant to rate magnitude at all. Chapters 7 and 8 provide detailed lists of links with high or unknown magnitude, which may comprise areas of significant uncertainty for species management. The CEM includes links with unknown magnitude based on established ecological principles and knowledge of particular features of frog biology and ecology in general for which there currently is no documentation for LLFR or any closely related species in particular. Specifically:

- The CEM identifies seven potential links among life-stage outcomes across the three LLFR life stages, all rated low for understanding. Of these seven, all but one is rated as unknown for link magnitude. The one exception is the relationship between adult survival and adult fertility, which warrants a rating of high for magnitude based on basic biological principles.

- The CEM identifies 24 potential links between critical biological activities and processes and life-stage outcomes across the 3 LLFR life stages that are rated low for understanding and either high or unknown for magnitude. As shown in chapter 7 (table 14), 16 of these 24 links are rated as unknown for link magnitude. For example, the CEM recognizes that chemical stress can impair growth in all three life stages, based on basic biological principles, but also recognizes that the literature provides no clues on whether or to what magnitude this relationship may affect LLFR in any life stage.

- The CEM identifies 27 potential causal links between habitat elements and critical biological activities and processes across the 3 LLFR life stages for which the available information suggested a rating of low for understanding and a rating of either high or unknown for magnitude. As shown in chapter 7 (table 15), 14 of these 27 links are specifically rated as unknown for link magnitude. These 14 links include proposed effects of birds and mammals and fish and herpetofauna on competition in the adult life stage; proposed effects of the fire regime on thermal stress in all three life stages; proposed effects on fish and herpetofauna on foraging by LLFR larvae and adults; proposed effects of monitoring, capture, and handling on both hydration stress and mechanical stress in all three life stages; and proposed effects of monitoring, capture, and handling on larval and juvenile resting/hiding behavior.

Finally, the CEM also identifies several potentially important causal relationships with high magnitude *and high or medium understanding*. These links represent the best-understood aspects of LLFR ecology. Their medium and high ratings for link understanding reflect cumulative knowledge from several detailed studies of

LLFR and their habitat, including the several studies by the AZGFD in the lower Colorado River, Bill Williams, Agua Fria, and Verde River valleys. These better understood, high-magnitude relationship include:

- For the larval-juvenile life stage, proposed high-magnitude links with medium understanding concerning the effects of infectious agents on disease and the effects of fish and herpetofauna on predation.

- For the adult life stage, proposed high-magnitude links with medium understanding concerning the effects of water temperature on mating and ovipositing, the effects of substrate texture and stability on adult resting/hiding behavior, and the effects of the hydrologic regime on occupancy and inter-site movement.

- For the adult life stage, proposed high-magnitude links with high understanding concerning the effects of infectious agents on disease; the effects of woody vegetation on mating and ovipositing, resting/hiding, and occupancy and inter-site movement; the effects of herbaceous vegetation on mating and ovipositing and occupancy and inter-site movement; and the effects of monitoring, capture, and handling on adult resting/hiding behavior, and vice versa.

- For the adult life stage, proposed high-magnitude links with medium understanding concerning the effects of competition and predation on occupancy and inter-site movement.

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for the lowland leopard frog (*Rana = Lithobates yavapaiensis*[3]) (LLFR). The purpose of this model is to help the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Bureau of Reclamation (Reclamation), identify areas of scientific uncertainty concerning LLFR ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure LLFR 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 present LLFR population and its distribution within the greater lower Colorado River (LCR) ecosystem in Reaches 3–7 along the main stem river and within the Bill Williams River watershed. Although LLFR currently occur only in the Bill Williams River watershed, LLFR occurred historically across the larger expanse, and recent studies indicate the presence of habitat that potentially could support LLFR (see below, this chapter). The model addresses the landscape as a whole rather than any single managed area.

The basic sources of information for the present CEM consist of the most recent LCR MSCP species account (LCR MSCP 2016) and the online account by Sredl (2018), which updates information from Sredl (2005). These two publications summarize and cite large bodies of earlier studies. Where appropriate and accessible, those earlier studies are directly cited, particularly Sredl et al. (1997a) and Sartorius and Rosen (2000). The CEM also integrates information from the Arizona Game and Fish Department (AZGFD) Heritage Data Management System Animal Abstract for LLFR (AZGFD 2006); websites; recent journal articles; reports by the AZGFD to the LCR MSCP (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Miller and Cotten 2016; Miller and Leavitt 2015; Leavitt et al. 2017; O'Donnell and Leavitt 2017a, 2017b); studies of LLFR in other areas (Rosen et al. 2013; Swann and Wallace 2010; Wallace et al. 2010); studies of closely related leopard frog species in the Southwestern United States, particularly the Chiricahua leopard frog (*Rana = Lithobates chiricahuensis*[2]) (AZGFD 2015; Hinderer et al. 2017; Sredl and Jennings 2018) and relict leopard frog (*Rana = Lithobates onca*[2]) (AZGFD 2003; Goldstein et al. 2017; Jaeger et al. 2017; Oláh-Hemmings et al. 2010); general works on the types of southwestern aquatic and wetland settings in which LLFR can occur; and the expert knowledge of LCR MSCP biologists. However,

[3] Use of the "Lithobates" nomenclature to replace "Rana" is controversial (Sredl 2018). The formal designation in the present document follows AZGFD (2006) and NatureServe (2018).

the purpose of the present report is not to provide an updated literature review; rather, its purpose is to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

This document is organized as follows: The remainder of chapter 1 provides a general description of the reproductive ecology of LLFR, describes the purpose of the CEM, and introduces the underlying concepts and structure of the CEM. Succeeding chapters present and explain the CEM for LLFR within the LCR and identify possible implications of this information for management, monitoring, and research needs.

LOWLAND LEOPARD FROG REPRODUCTIVE ECOLOGY

LLFR are year-round residents of the Southwestern United States, currently distributed in clusters of occurrences in the northern, eastern, and extreme southeastern tributary watersheds to the Gila River in central and southeastern Arizona and western New Mexico; and in the Bill Williams River watershed, tributary to the LCR (AZGFD 2006; Cotten and Leavitt 2014; LCR MSCP 2016; Sredl 2018). Historically, LLFR occurred from sea level to approximately 6000 feet elevation (approximately 1,800 m) throughout the Gila River Basin in Arizona and New Mexico; along the LCR from the Gila River confluence southward into Mexico and northward perhaps as far as Reach 3, as well as throughout the LCR tributary Bill Williams River watershed; and from the Gila River confluence with the LCR westward into the Coachella and Imperial Valleys in California and Mexicali Valley in northern Baja California, Mexico (AZGFD 2006; LCR MSCP 2016; Oláh-Hemmings et al. 2010; Sredl 2018). A small and apparently long-established population also occurs in Surprise Canyon, a tributary to the Colorado River in the western Grand Canyon approximately 40 river miles upstream of Lake Mead (Oláh-Hemmings et al. 2010). Differences in mitochondrial deoxyribonucleic acid (mtDNA) between the Surprise Canyon population and LLFR across the rest of their range indicate that the two populations most likely separated in the Middle Pleistocene. The mtDNA of the Surprise Canyon and main LLFR populations also both differ similarly from the mtDNA of the relict leopard frog, all populations of which occur immediately to the north and west of Lake Mead (Oláh-Hemmings et al. 2010). The mtDNA data indicate that the LLFR and relict leopard frog most likely diverged from a common ancestor in the Early Pleistocene (Oláh-Hemmings et al. 2010). Recent systematic surveys along the LCR below Davis Dam and up the Bill Williams River (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Miller and Cotten 2016; Miller and Leavitt 2015; Leavitt et al. 2017; O'Donnell and Leavitt 2017a, 2017b) have found LLFR only in the

Bill Williams River watershed, both below Alamo Lake along the Bill Williams River main stem both downstream and upstream of Planet Ranch and above the lake on its main tributary, the Big Sandy River.

The major species accounts (see chapters 2–4) document that LLFR occupy a variety of relatively shallow, low-velocity lotic, lentic, and wetland aquatic habitats, including artificial water bodies such as cattle watering ponds (*aka* "cattle tanks"). They remain active year round at lower elevations and in waters fed by geothermal springs but become inactive during winter at higher elevations. They may mate and produce egg masses (*aka* clutches) at any time of the year at lower elevations or in waters fed by geothermal springs but otherwise reproduce mainly in early to mid-spring (March – April), with a secondary peak in fall.

One study (Sartorius and Rosen 2000) reports that clutch volumes oviposited early in the spring breeding season were smaller than those oviposited late in the season; otherwise, no studies have assessed the number of LLFR eggs per clutch. However, two related species may provide analogs: Sredl and Jennings (2018) cite unpublished data on clutch sizes of 300–1,485 eggs among Chiricahua leopard frogs. The LLFR originally was considered a lowland variety of the northern leopard frogs (*Rana = Lithobates pipiens*) but later reclassified (Platz 1988). The latter species produces clutches with 645–7,648 eggs (Rorabaugh 2018a).

One study found that LLFR larvae emerge from their eggs after 15–18 days following oviposition, with the rate of maturation likely varying with water temperature, based on data for closely related species in the region (Zweifel 1968). Spring-born larvae metamorphose in 3–4 months, while fall-born larvae may overwinter and metamorphose only the following spring. Drier years may result in faster development to metamorphosis among spring-born larvae (Sartorius and Rosen 2000). Evidence from a study of the relict leopard frog suggests that the rate of maturation of LLFR larvae to metamorphosis likely also varies with water temperature (Goldstein et al. 2017).

LLFR reproductive ecology evolved in adaptation to the unique climate of the hot southwestern desert. As Sartorius and Rosen (2000) summarize, precipitation and runoff across the historic range of LLFR

> *… follows the bimodal Sonoran pattern … with peaks in summer (July – August) and winter (December–January) separated by a highly predictable foresummer drought …. Summer storms tend to be localized and strong and often cause flash floods in small drainages. Winter rains are characteristically widespread and more prolonged, producing long periods of high stream discharge in wet years rather than the brief, unpredictable, scouring spates seen in summer. Presence of stable, flowing water in the stream is most predictable during late winter to early spring; and less so during summer, when prolongation of the summer dry period may lead to habitat drying, or onset of summer thunderstorms often produce flash floods.*

The region also experiences significant year-to-year variation in the magnitude and timing of rainfall both regionwide and between localities within the region. Air temperatures and associated evapotranspiration follow a more consistent, unimodal pattern with a prolonged summer peak. The rate of evapotranspiration from a water body and its surrounding vegetation determines how quickly the water dries down following each input of fresh water.

Sartorius and Rosen (2000) summarize the reproductive ecology of LLFR in this predictably variable hydrologic setting:

> *Eggs hatch primarily in late March with a few lasting as late as May. Water levels in perennial pools usually begin to drop in mid-May and reach seasonal lows just before the onset of summer rains, usually in early July. Thus, mobile tadpoles or metamorphs and not immobile egg masses, are exposed to the summer drought. Egg masses are absent also from the summer flash flooding season in late July through early September. Floods would undoubtedly wash egg masses downstream into unsuitable low desert habitats that quickly dry after storms. Summer rains also provide a potential dispersal opportunity for metamorphs. Tadpoles that hatch in spring enjoy a warm and food-rich summer and grow rapidly to metamorphosis, or at least to a size at which they can survive moderate summer flooding. Tadpoles that hatch in fall may share some of the benefits of spring hatchlings, including avoidance of summer drought and late summer flood scour.*

LLFR adaptation to this predictably variable hydrologic setting thus includes breeding without the need for cues from precipitation, and may also include some plasticity in larval development, resulting in faster larval development under drying conditions. LLFR adaptation also includes behaviors that allow it to successfully live in this hydrologically variable setting: LLFR adults have been observed to disperse downstream in runoff pulses and move overland to other sites; find refuge in mud cracks, mammal burrows, or rock fissures; quickly reoccupy a location when water returns; and reproduce in large numbers (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014; Sartorius and Rosen 2000; Sredl 2018; Sredl et al. 1997a; Swann and Wallace 2010; Wallace et al. 2010). These behaviors result in a high level of variability in LLFR occupancy and abundance within and between watersheds (Rosen et al. 2013; Sredl et al. 1997a, 1997b; Wallace et al. 2010).

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.

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

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

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

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

- **Habitat elements** – These consist of the specific habitat conditions, the quality, abundance, and spatial and temporal distributions of which significantly affect the rates of the critical biological activities and processes for each life stage. These effects on critical biological activities and processes may be either beneficial or detrimental. Taken together, the suite of natural habitat elements for a life stage is called the "habitat template" for that life stage. Defining the natural habitat template may

involve estimating specific thresholds or ranges of suitable values for particular habitat elements, outside of which one or more critical biological activities or processes no longer fully support desired life-stage outcome rates—if the state of the science supports such estimates.

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

The process of identifying the life stages, life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors for a CEM begins with a review of the LCR MSCP and other major accounts for the species of interest, accounts for better known but closely related or ecologically similar species, and LCR MSCP management concerns as expressed in the LCR MSCP Habitat Conservation Plan (HCP) (Reclamation 2004) and annual work plans (LCR MSCP 2018a). The process also follows conventions for life history CEMs focused on individual species and their population dynamics in the relevant branch of zoology for the species of interest. Further, the process is guided by an overarching need to ensure that the CEM helps the LCR MSCP identify areas of scientific uncertainty concerning the ecology and specific habitat requirements of the species it has been charged with conserving, the effects of specific stressors on these species, the effects of specific management actions aimed at habitat and species conservation, and the appropriate methods with which to monitor species and habitat conditions. Each CEM is developed in consultation with experts in the LCR MSCP, and submitted in draft form for review by the LCR MSCP, 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 LCR 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 care or the production of viable newborn in the presence of parental care. This third possibility pertains either to a life stage in which all individuals participate in reproduction, or to a life stage that focuses only on some subset of adults that engages in reproduction in a single year, such as "Breeding Adult." Several of the species of concern to the LCR MSCP are subject to management goals concerning their genetic integrity. However, the present 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 activities or processes for one life stage also may affect dynamics in the next life stage. Most commonly, such transgenerational 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 activities for breeding adult birds that have energetic and other costs for these adults. At the same time, these activities constitute crucial features of the environment—i.e., habitat elements—for the eggs and nestlings that affect their access to food and vulnerability to predators.

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

The process of identifying the habitat elements for each life stage in a CEM focuses on identifying physical or biological environmental conditions that: (1) are necessary or beneficial for the successful participation of individuals of a life stage in particular beneficial critical biological activities or processes, (2) may limit or prevent the successful participation of individuals of a life stage in particular beneficial critical biological activities or processes, or (3) may result in the participation of individuals of a life stage in particular detrimental critical biological activities or processes. Habitat elements thus shape the rates of beneficial or detrimental critical biological activities or processes. Further, habitat elements may affect critical biological activities or processes directly, indirectly through their effects on other habitat elements, or both. For example, the herbaceous vegetation in a marsh may benefit an aquatic species directly by providing protective cover and plant litter on which the aquatic species may feed, or indirectly by helping maintain cooler water temperatures, stabilizing the marsh substrate, and providing habitat for insects on which the aquatic species also may feed. However, the same marsh vegetation may also provide habitat for invertebrate or vertebrate species that may prey on the aquatic species of interest.

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

Finally, the process of identifying the controlling factors for each life stage in a CEM focuses on environmental conditions and dynamics—including human actions—that (1) determine the quality, abundance, and spatial and temporal distributions of important habitat elements and (2) are within the scope of potential human manipulation, most particularly manipulation by the LCR MSCP and its conservation partners along the LCR valley. The specific or "immediate" controlling factors identified in a CEM necessarily exist and vary in a larger context of human institutions and policies and both short- and long-term dynamics of climate and geology; however, the CEM does not address this larger context. The process of identifying the controlling factors for each life stage in a CEM also recognizes that a controlling factor may affect a habitat element directly or may do so indirectly through its effects on either another controlling factor or another habitat element.

The process of identifying the controlling factors for each life stage in a CEM also recognizes that the key drivers affecting the habitat elements for that life stage can be combined or split into different categories in different ways. A single controlling factor may encompass several more specific variables or human activities. There is no rule for how many controlling factors a CEM must include. The process of identifying the controlling factors for each life stage in a CEM lumps together types of human activities in particular that closely covary with

each other over space and time along the LCR because of the institutions and policies driving them and/or because these activities strongly interact with each other and, therefore, are not independent. A CEM also may lump together human activities when there is not sufficient knowledge to split these into separate categories in ways that would help the LCR MSCP manage the species of concern. Finally, the CEMs lump together human activities as controlling factors when these activities have similar effects or management implications across multiple life stages and across multiple species of concern to the LCR MSCP even if these effects or implications differ in their details between life stages and species. Lumping together such closely related activities under the heading for a single controlling factor across multiple species and multiple life stages of these species makes comparison and integration of the CEMs across the LCR MSCP less difficult.

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

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

Chapter 2 – LLFR 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 LLFR within the LCR on which to build the CEM. Except where noted, the sources for the following information are Platz (1988), the AZGFD Heritage Data Management System Animal Abstract for LLFR (AZGFD 2006), the most recent LCR MSCP species account (LCR MSCP 2016), and the online account by Sredl (2018). Table 1 and figure 1 summarize the proposed LLFR life-stage model.

Table 1.—LLFR life stages and life-stage outcomes

Life stage	Life-stage outcomes
1. Eggs	• Egg growth • Egg survival
2. Larvae and juveniles	• Larval-juvenile growth • Larval-juvenile survival
3. Adults	• Adult growth • Adult survival • Adult fertility • Gene flow

INTRODUCTION TO THE LLFR LIFE CYCLE

The LLFR life cycle is typical of many amphibians, with aquatic egg, larval, and juvenile phases, each with its own distinctive suite of behaviors and developmental transformations, followed by metamorphosis to an adult amphibious (or terrestrial) stage. Once transformed into their adult body form, both males and females continue to grow, as measured by body weight and snout-vent length (SVL), both before and after reaching sexual maturity. The LLFR conceptual ecological model generally follows Gosner (1960) in distinguishing three life stages—eggs, larvae and juveniles (metamorphs), and adults. The authors of the present CEM considered distinguishing separate LLFR larval and juvenile life stages but found insufficient evidence on which to base such a distinction; evidence in the future may support such a finer distinction. The literature does not suggest any need to distinguish a separate hatchling stage between egg and larva for LLFR, as may occur in some anurans (Gosner 1960; Alford 1999).

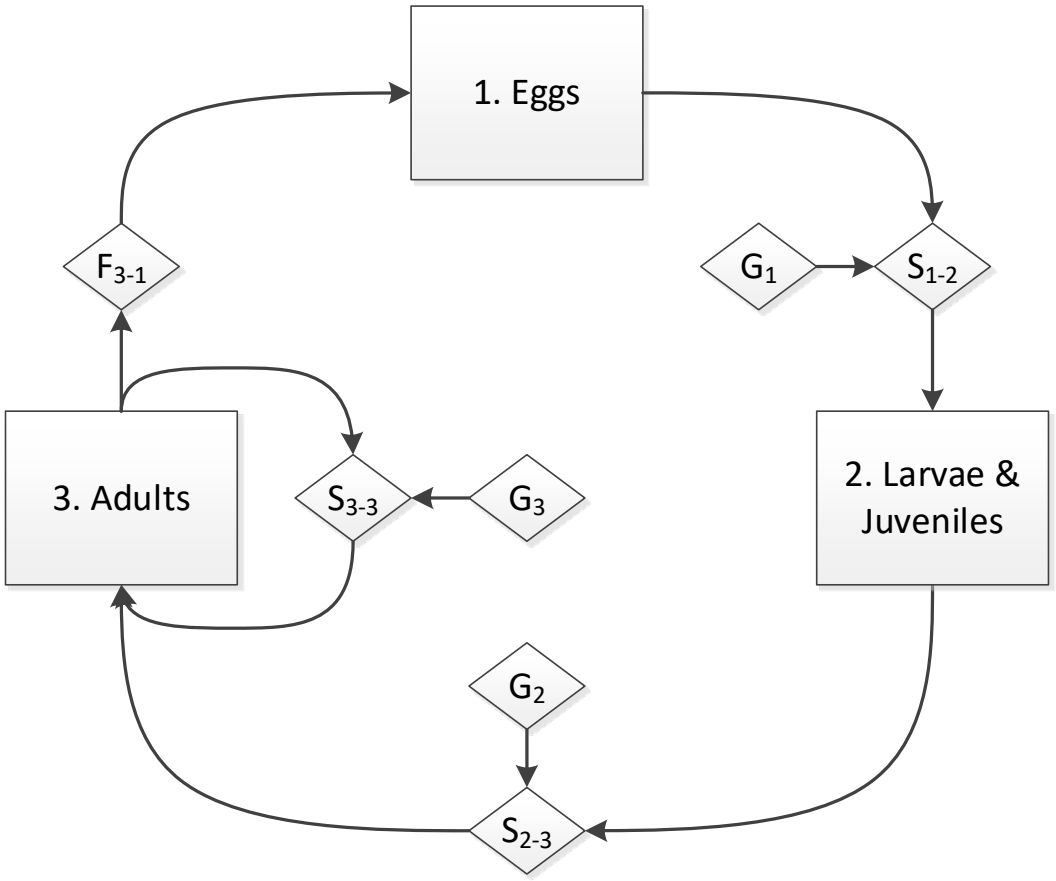

Figure 1.—Proposed LLFR life history model.
Explanation of figure 1: Squares indicate life stages, diamonds indicate life-stage outcomes, and arrows indicate life-stage transitions. In the diamonds, S = survival, G = growth, and F = fertility; subscripts indicate the life stages involved in each transition. Gene flow is not strictly an aspect of life history; therefore, it is not illustrated.

The LLFR conceptual ecological model for each of these three life stages recognizes a minimum of two life-stage outcomes: growth and survival. "Growth" in this context refers both to changes in body size (length, weight) and to transformations in body structure and function (metamorphosis). Growth may be positive or negative and may occur at different rates in females versus males. For example, Sredl et al. (1997a) report seasonal fluctuations in adult SVL among both males and females at two sites in Arizona, with higher positive growth rates in males compared to females. "Survival" for eggs and larvae-juveniles in the LLFR conceptual ecological model refers to the rate at which members of a local population survive through their entire life stage to enter—recruit to—the next life stage. "Survival" for adults in the LLFR conceptual ecological model refers to the rate at which individuals in a local population survive from year to year. LLFR are estimated to have an overall life span of 3 years (see below).

The LLFR conceptual ecological model recognizes fertility as an additional life-stage outcome for the adult stage. "Fertility" in the LLFR conceptual ecological model refers to the rate of production of viable fertilized eggs per adult female.

Finally, the LLFR conceptual ecological model recognizes concerns expressed in the literature over tendencies toward genetic isolation among LLFR local populations as a result of habitat loss and drainage network fragmentation. "Genetic isolation" and the related concept of "gene flow" refer to the rate at which local populations exchange deoxyribonucleic acid (DNA) through the movement and mating of individuals from different natal populations. Gene flow affects the genetic diversity of local populations. The greater this diversity, the greater the possibility that individuals of a given life stage will have genetically encoded abilities to survive their encounters with the diverse stresses presented by their environment and/or take advantage of the opportunities presented (Allendorf and Leary 1986). CEMs focused on the dynamics of species abundance and geographic distribution typically do not address gene flow as a life-stage outcome; however, the LLFR conceptual ecological model does address this matter to recognize the importance it may have for overall population viability. Specifically, the LLFR conceptual ecological model recognizes gene flow among local populations and meta-populations as a life-stage outcome for the adult life stage. This outcome appears in table 1, but does not appear in figure 1, because the figure illustrates the LLFR life history, and gene flow is not strictly an aspect of life history.

LLFR LIFE STAGE 1 – EGGS

The LLFR egg stage begins when adult females deposit their eggs in a water body (e.g., pond, stream pool, marsh, etc.). As discussed below, mating (including fertilization) and ovipositing are critical biological activities in the adult life stage. The LLFR egg stage ends when the embryos emerge from their natal egg mass as larvae, also known colloquially as tadpoles or pollywogs. As noted above, the literature does not indicate a separate hatchling stage (Alford 1999; Gosner 1960;) between LLFR egg and larval development.

LLFR attach their egg masses to aquatic vegetation, bedrock, or gravel close to (within 2 centimeters [cm]) or at the water surface (Sartorius and Rosen 2000). Because they are attached to non-floating materials, the egg masses do not rise or fall with changes in water depth. Consequently, eggs near the top of an individual mass are at greater risk of exposure to air. Sartorius and Rosen (2000) found low rates of mortality among LLFR eggs within individual egg masses except among those near the top of the mass that became exposed to air.

The literature does not report information on LLFR clutch sizes (numbers of eggs per clutch). Two related species may provide analogs: Sredl and Jennings (2018)

cite unpublished data on clutch sizes of 300–1,485 eggs in the closely related Chiricahua leopard frog. The LLFR originally was considered a lowland variety of the northern leopard frog but later reclassified (Platz 1988). The latter species produces clutches with 645–7,648 eggs (Rorabaugh 2018a).

Other species presumably consume LLFR eggs, although the literature does not include any formal or anecdotal studies of the topic. Microcosm experiments by Fernandez and Rosen (1996) identified the non-native virile or northern crayfish (*Faxonius = Orconectes virilis*) as a predator of Arizona native amphibian eggs, larvae, and adults. These findings are consistent with reports worldwide of crayfish as predators of amphibian eggs and larvae. All species that consume LLFR larvae (see below) potentially could consume LLFR eggs as well. The discussions of birds and mammals, fish and herpetofauna, and macroinvertebrates in chapter 4 further address possible predators of LLFR eggs.

LCR MSCP (2016) and Sredl (2018) summarize numerous studies indicating that LLFR may deposit egg masses from January into May, and September through October, but with a large peak in ovipositing activity from March to May, a smaller peak in September – October, and a distinct hiatus between these two peaks. Sartorius and Rosen (2000) found that eggs deposited early in the first peak season were about twice the size of those deposited later in the same season, before the summer hiatus. Winter deposition of egg masses may be associated with warm water temperatures, such as in spring-fed pools or streams.

Water temperature may also affect egg development. Ruibal (1962 *in* Sredl 2018) observed upper and lower thermal limits for LLFR egg development of 29 degrees Celsius (°C) and 11 °C, respectively, in a population in southern California. It should be noted that, at the time Ruibal (1959, 1962 *in* Sredl 2018) carried out his study, LLFR were not recognized as a separate species but rather as the "lowland variety" of the northern leopard frog," later reclassified as LLFR (Platz 1988). As noted in chapter 1 (see "Lowland Leopard Frog Reproductive Ecology"), a study by Zweifel (1968) suggests that the rate of maturation of LLFR eggs likely varies with water temperature based on data for closely related species in the region. Evidence from a study of the relict leopard frog similarly suggests that the rate of maturation of LLFR larvae to metamorphosis likely also varies with water temperature (Goldstein et al. 2017).

Water salinity also affects LLFR egg development. In the same study in southern California that examined LLFR egg maturation in different water temperatures, Ruibal (1959 *in* LCR MSCP 2016) found that salinities > 2.5 parts per thousand (‰) always caused some defect or abnormality in developing LLFR eggs, salinities between 3.8 and 4.6‰ were semilethal, and salinities > 5‰ were lethal.

LLFR egg maturation into larvae has been observed to require 15–18 days in the wild (Sartorius and Rosen 2000). Among frogs in general, embryos in their natal egg mass are vulnerable during this period to predation, infection and parasites, effects of solar radiation and/or exposure, dehydration, displacement or burial by

a flood pulse, effects of elevated water temperatures, or reduced oxygen levels (Alford 1999; Duellman and Trueb 1986). Effects from these stressors range from delayed development to outright mortality. Growth and survival through the egg stage, among anurans in general, also vary with the behavior and condition of the female parent. As discussed below (see "LLFR Life Stage 3 – Adults"), female age and body size, among other factors (Stebbins and Cohen 1995; Wells 2007 and references therein) affect clutch size for many anuran species. In addition, the type(s) of locations selected by males or females for ovipositing may differ in egg vulnerability to predation or exposure; however, no investigators have looked for these possible interactions specifically in LLFR.

LLFR LIFE STAGE 2 – LARVAE AND JUVENILES

This life stage begins when the eggs hatch and the newly hatched larvae swim away from the remains of their natal egg mass as tadpoles with eyes, a tail, and external gills. As noted above, the literature does not report the occurrence of a separate intervening hatchling stage for LLFR, such as Gosner (1960) reports among some anurans. As do all frog species, LLFR undergo several types of transformations during their brief larval-juvenile life stage, culminating in a final metamorphosis into adults. Platz (1988) reports that LLFR larvae at the start of this final metamorphosis have an average length of 25–29 millimeters (mm). Rorabaugh (2018b) states that LLFR larvae grow 75–90 mm "… prior to metamorphosis." This life stage ends with the completion of metamorphosis (i.e., when the frogs fully attain their adult body form and physiology).

The authors of the present CEM considered distinguishing the final, most substantial phase of metamorphosis as a separate "juvenile" life stage for three reasons. First, frogs in the midst of the final phase of metamorphosis do not forage, as do both frog larvae and adults, but rather obtain all their nutrition through resorption of their tails. Second, frog juveniles that have begun or are in the midst of metamorphosis, either developing forelegs or still retaining part of their tails, are particularly vulnerable to predation due to their "diminished locomotor capacity" (Hoff et al. 1999; Wassersug and Sperry 1977). Duellman and Trueb (1986) similarly note that, while larval survivorship in amphibians is low in general, the transformation through metamorphosis is particularly challenging. Third, the literature on LLFR occasionally (although rarely) distinguishes information on juveniles from information on adults (Ruibal 1962 *in* Sredl 2018; Seim and Sredl 1994 *in* AZGFD 2006). However, the literature on LLFR mostly does not provide information on juveniles—let alone threats to them—separately from information on LLFR larvae. Consequently, evidence in the future may support distinguishing a juvenile life stage separately from the larval life stage, but the present CEM does not.

The Sredl (2018) species account for LLFR states the following:

> *Altig et al. (1998) describe the tadpoles of lowland leopard frogs… Tadpoles may metamorphose in the same year they were oviposited or overwinter (Collins and Lewis 1979), and length of larval period may be as short as 3–4 mo or as long as 9 mo (unpublished data). Jennings (1990) found that tadpoles of Chiricahua leopard frogs in warm springs appeared to grow continuously, while growth of those in cold water sites appeared to be arrested during the winter. Lowland leopard frog tadpoles would likely exhibit the same pattern (R. Jennings, personal communication).*

Overwintering is common among ranid frog larvae in colder temperate climates; however, overwintering success depends on an absence of freezing and/or anoxia (Tattersall and Ultsch 2008). More broadly, water temperature likely affects the rate of growth of LLFR during this life stage, the brevity of this life stage, and survival through the life stage based on evidence from the closely related relict leopard frog. Specifically, Goldstein et al. (2017) report:

> *Relict leopard frog … tadpoles were obtained shortly after hatching at Gosner stage 25 and raised in aquaria maintained at 15, 20, 25, 30 and 35 °C. Development was arrested in the 15 °C group, and survivorship declined to 64% after 191 days. However, 80% of the surviving larvae remained alive after the temperature was increased to 25 °C. Of these, 96% reached metamorphosis. Survivorship of the 20, 25 and 30 °C acclimation groups was 82, 94 and 66%, respectively, whereas none survived at 35 °C. Time to metamorphosis was significantly shorter for the 25 °C group (67 ± 1 days), followed by the 30 °C (98 ± 2 days) and 20 °C (264 ± 7 days) groups.*

The final metamorphosis of frog larvae into adults involves significant hormonal and physical changes. Beginning with the emergence of both hindlimbs and forelimbs, the legs continue to develop as the tail disappears; bone replaces cartilage; the shape of the skull, and particularly the jaw, change to an adult morphology; lungs develop in place of gills; and the digestive system transforms from one adapted to herbivory to a carnivorous diet (Duellman and Trueb 1986; Gilbert 2000; Wells 2007). As also noted above, LLFR juveniles may undergo metamorphosis in the same year they were oviposited or in the next year if they overwinter. Sartorius and Rosen (2000) report LLFR metamorphosis beginning earlier in drier years than in wetter years.

LLFR larvae are completely aquatic. As with all frog larvae, they breathe through their gills, propel themselves with their tails, and rest by attaching themselves to aquatic vegetation, substrates, or debris using their mouths. Marti and Fisher (1998) report that LLFR larvae are herbivorous, feeding on algae, organic debris, plant tissue, and micro-organisms. Sartorius and Rosen (2000) report observing LLFR larvae feeding on filamentous algae (*Cladophora*) mats and small organisms within them; however, the literature reviewed for this CEM does not

otherwise record any studies of feeding behavior or diet among LLFR larvae. As noted above, frog larvae do not feed at all during the final phase of their metamorphosis.

Several of the major species accounts for LLFR (LCR MSCP 2016; Sredl 2018; Sredl et al. 1997a) point to a lack of information concerning predation on LLFR in any life stage, and they identify this as a crucial gap in knowledge. The literature on LLFR includes only two formal studies of predation on LLFR larvae. In a study along two desert streams in Arizona, Jones (1990 *in* Sredl 2018) found that adult and subadult black-necked garter snakes (*Thamnophis cyrtopsis*) consumed adult and larval LLFR more frequently than any other prey species. The study did not distinguish juveniles as a separate life stage. Its findings that adult and subadult black-necked garter snakes consumed adult and larval LLFR more frequently than any other prey species therefore likely indicates intense predation on LLFR juveniles as well.

Rosen et al. (2013) studied the consumption of LLFR larvae under laboratory conditions by non-native predatory fishes collected in southern Arizona. The non-native predatory fishes included in the study consisted of black bullhead (*Ameiurus melas*), channel catfish (*Ictalurus punctatus*), green sunfish (*Lepomis cyanellus*), bluegill (*Lepomis macrochirus*), largemouth bass (*Micropterus salmoides*), flathead catfish (*Pylodictis olivaris*), and redbelly tilapia (*Tilapia zillii*). All seven non-native predatory fishes readily consumed LLFR larvae. Cotten and Leavitt (2014) assessed the extent to which the presence of several classes of predators predicts LLFR habitat use along the LCR (Reaches 3–7) and along the Bill Williams River below Alamo Dam and found that the presence of sunfish (*Lepomis* spp.) and largemouth bass strongly suppress LLFR numbers in this study area. Sredl et al. (1997b) also specifically identify non-native bass (*Micropterus* spp.) and sunfish as predators of LLFR larvae.

Additional evidence points to several other individual species as likely predators of LLFR larvae, particularly in the greater LCR ecosystem. The northern Mexican gartersnake (*Thamnophis eques megalops*) occurs along several reaches of the Bill Williams River and its main tributary above Alamo Lake, the Big Sandy River (Cotten and Grandmaison 2013; Cotten et al. 2015; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a). The U.S. Fish and Wildlife Service (USFWS) and Reclamation recently added the northern Mexican gartersnake to the LCR MSCP as a covered species (USFWS and Reclamation 2018). Sabin (2018) summarizes numerous reports of this gartersnake feeding on larvae of LLFR and other southwestern leopard frogs. Cotten et al. (2015) note that the frequency of captures of this gartersnake in funnel traps along the Bill Williams River in 2012 were "associated with amphibian metamorphosis." However, O'Donnell and Leavitt (2017a) note an absence of direct field observations of northern Mexican gartersnakes feeding on LLFR.

American bullfrog (*Rana = Lithobates catesbeiana*) larvae and adults and the non-native northern crayfish are widely suspected as predators of one or more LLFR life stages (Sredl et al. 1997b). Otherwise, the LCR MSCP (2016) reports that suspected predators of LLFR larvae include "… insects (Belostomatids, Notonectids, Dytiscids, and Anisopterans), vertebrates (native and non-native fishes, tiger salamanders (*Ambystoma tigrinum*), garter snakes (*Thamnophis* spp.), mud turtles (*Kinosternon sonoriense*), great blue herons (*Ardea herodias*), and other birds."[4] The discussions of birds and mammals, fish and herpetofauna, and macroinvertebrates in chapter 4 further address possible predators of LLFR larvae and juveniles.

Seim and Sredl (1994 *in* AZGFD 2006) report finding LLFR juveniles more often in small pools and marshy areas, versus adults, more frequently in pools. The study authors suggest that the small pools and marshy areas better supported juvenile survival compared to the large pools; however, the specific reasons for this difference were not apparent.

Sredl et al. (1997a) used the results of mark-recapture studies at several sites in Arizona from 1991 to 1996 to calculate rates of survival among LLFR juveniles and adults at two sites in particular: the Big Spring site in Graham County and the Tule Creek site in Yavapai County. The latter is the type locality for the original definition of the species (Platz 1988). The study found a consistently higher rate of survival among adults compared to juveniles at the two sites: Adult survivorship at Big Spring ranged from 0.06 to 1.72, while juvenile survivorship ranged from 0.03 to 1.83; adult survivorship at Tule Creek site ranged from 0.04 to 3.92, while juvenile survivorship ranged from 0.08 to 2.09. Survivorship at both sites seemed to follow a seasonal pattern for both juveniles and adults: higher in spring and summer, lower in fall and winter, with winter survivorship consistently the lowest.

The mark-recapture study by Sredl et al. (1997a) also identified some event-specific causes of elevated mortality, including a significant flood event and an outbreak of chytridiomycosis (chytrid fungus disease; see chapter 3, "Diseases") that was diagnosed only retroactively (Sredl 2018). This outbreak of chytrid fungus disease affected juveniles more severely than it affected adults, and "[r]eduction in total habitat area due to siltation of several important pools preceded and may have exacerbated the die-off" (Sredl 2018).

LLFR growth and survival during this life stage thus depend minimally on water temperatures, foraging success prior to the final phase of metamorphosis,

[4] The section of chapter 3, "Predation," provides further information on potential predators of LLFR (also see chapter 4, "Birds and Mammals," "Fish and Herpetofauna," and "Macroinvertebrates"). The list of suspected predators of LLFR juveniles in the LCR MSCP species account (2016) is the same as in Sredl (2018); neither provides a citation for the original source of the information. As noted by several authors (LCR MSCP 2016; Sredl 2018; Sredl et al. 1997a), there is little direct evidence of a particular species preying on LLFR in any life stage.

predation rates, disease, and the persistence of their habitat versus loss due to drying out or flood disturbance or burial (Alford 1999). Presumably, as aquatic organisms in a desert environment, their growth and survival rates also depend on their exposure to environmental contaminants and to low levels of dissolved oxygen (DO) as a result of water stagnation, depending on the type(s) of aquatic habitat present at their natal site (Alford 1999).

LLFR LIFE STAGE 3 – ADULTS

The LLFR adult life stage begins with the completion of juvenile metamorphosis and lasts through the remainder of the frog's life. LLFR adults initially are sexually immature and reach sexual maturity only after additional growth and hormonal changes. The literature does not indicate how quickly LLFR adults may reach sexual maturity. AZGFD (2006) reports unpublished data that "[t]he smallest males to exhibit secondary sexual characteristics from study sites in Graham and Yavapai counties, Arizona were 53.5 mm (2.1 in[ches]) and 56.2 mm (2.2 in[ches]) SVL, respectively." Platz (1988) reports adult sizes of 46–72 mm SVL among males and 53–87 mm SVL among females in general. Based on skeletal chronology, LLFR adults live up to 3 years in the wild (AZGFD 2006; Sredl et al. 1997a).

LLFR adults presumably are carnivorous, preying on arthropods and other invertebrates, as do all western leopard frogs (Degenhardt et al. 1996 *in* AZGFD 2006; Stebbins 1951; Stebbins 1985 *in* AZGFD 2006). LLFR adults may also cannibalize LLFR larvae (see above, "LLFR Life Stage 2 – Larvae and Juveniles"). AZGFD (2006) also notes that "Stomach analyses of other [adult] members of the leopard frog complex from the western United States show a wide variety of prey items, including many types of aquatic and terrestrial invertebrates (e.g., snails, spiders, and insects) and vertebrates (e.g., fish, other anurans [including conspecifics], and small birds)." However, no studies have specifically investigated the diet or foraging behaviors among LLFR adults (LCR MSCP 2016).

LLFR adults engage in mating behaviors—including calling behaviors—sufficiently different from those of related, sympatric species to maintain the overall genetic and evolutionary integrity of the species (Frost and Platz 1983; Platz 1988). However, LLFR in the wild can hybridize with related species, such as the Chiricahua leopard frog (AZGFD 2006) (see chapter 3), with which LLFR is sympatric along a zone where eastern portions of the LLFR range overlap western portions of the range of the Chiricahua leopard frog.

The literature indicates a sex ratio close to 1:1, when reported (Sredl et al. 1997a). As noted above, this chapter (see "LLFR Life Stage 1 – Eggs"), most LLFR mating occurs during two peak seasons: March into May, and September through

October. Sartorius and Rosen (2000) found that LLFR eggs deposited early in the first peak season were about twice the size of those deposited later in the same season.

LCR MSCP (2016) recognizes a "distinct hiatus" in breeding during summer, roughly May through August. However, Sredl (2018) alternatively states:

> *In most populations, breeding usually follows springtime emergence after a period of winter inactivity and continues through summer and into fall. Populations occupying geothermal springs or at low elevations are likely active year-round (R.D. Jennings, unpublished data). Egg masses have been observed from January through late April and October …. Reproductive activity may decrease between the time temperatures warm in mid-May to prior to the onset of the summer rains in early July).*

Studies of LLFR along the LCR have not clarified this picture of when LLFR breed in different environmental settings. LLFR surveys carried out in 2015 and 2016 along the Bill Williams River downstream from Alamo Dam, and along its main tributary, the Big Sandy River, upstream of Alamo Lake (Cotten and Leavitt 2016; Leavitt et al. 2017), took place only between February and April. A prior survey for LLFR along the Bill Williams River below the dam in 2011–13 took place only during spring (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014). On the other hand, surveys for Colorado River toads (*Incilius alvarius*) and their egg masses at the same locations during July 8 – October 4, 2014, and July 7 – October 6, 2015, did not detect any LLFR egg masses (Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b). The literature therefore does not indicate whether LLFR breed—or could breed—outside the spring season along the LCR, a low-elevation setting.

The literature reviewed for the present CEM does not provide evidence concerning the factors that cue LLFR mating. The major species accounts mention suggestions of rainfall and changes in water temperature as possible breeding cues for LLFR and related species in the Southwest, while noting an absence of direct investigations of the subject. The Sredl (2018) account quoted above implies that temperature—or change in temperature—is the dominant cue. The literature also does not indicate the number of times an individual female may breed in any single year or what factors may affect that number at a given location—longstanding gaps in knowledge (Platz 1988)—nor indicate what proportion of the male or female population participates in breeding in a given year or whether this proportion varies with any external factors.

Growth in metamorphs and adults can affect survival and mating success among frogs in general. For example, Berven (1990) found that larger wood frog (*Rana sylvatica*) metamorphs matured sooner, and were larger as adults, presumably due to greater success in foraging as larvae; and that survival in wood frogs was higher for those frogs that metamorphosed earlier and at larger sizes. Further,

larger adult wood frogs have higher likelihoods of mating (Howard and Kluge 1985) and produce both larger eggs and larger clutch sizes (Berven 1982). In fact, the size and age specifically of adult females of many frog species affect clutch size (Wells 2007). According to Stebbins and Cohen (1995), clutch size depends in part on genetics, nutritional condition of the female, the number of repetitive breedings, and the temperature and length of the growing season, among other factors. The location of oviposition sites selected by males or females may also affect egg vulnerability to predation or exposure. However, no investigators have specifically examined the possible effects of adult age or body size on LLFR survival, mating success, or clutch size.

The literature on LLFR does not include any observations of breeding migrations, a behavior found in other amphibians (Sredl 2018). However, LLFR adults do move between localities, thereby maintaining gene flow among local populations. The causes for such movement have not been studied systematically. Sredl (2018) states: "Little is known of seasonal migrations. In one case, following drying of a pond, 154 frogs moved about 250 m upstream to a pond that did not dry, while 4 frogs moved 900 m downstream." LCR MSCP (2016) states:

> *Lowland leopard frog populations are primarily connected by movement through drainages and not along straight lines (Goldberg et al. 2004). Goldberg et al. (2004) studied populations in Saguaro National Park and found distances between populations to range from 0.4 to 18.4 miles (0.7 to 29.7 km, respectively). Populations of this species are more isolated from each other than other amphibians in Arizona (Goldberg et al. 2004). Goldberg et al. (2004) found that genetic differentiation was high and migration low among populations in different drainages in the Tucson Basin of southern Arizona.*

Several studies in fact propose that LLFR exhibit significant genetic isolation among local populations within and between watersheds throughout their range (Goldberg et al. 2004 *in* LCR MSCP 2016; Oláh-Hemmings et al. 2010; Rosen et al. 2013; Savage et al. 2015), brought about by drainage network fragmentation (loss of connectivity), preventing adult movement between populations:

- Goldberg et al. (2004 *in* LCR MSCP 2016) present evidence supporting an inference that some of the LLFR subpopulations studied in the Rincon Mountains in Saguaro National Park (see quotation above) have experienced genetic bottlenecks.

- The analysis of mtDNA from 202 LLFR adults from 23 sites in Arizona and northern Mexico and 23 samples from the isolated population of LLFR in Surprise Canyon, Arizona, by Oláh-Hemmings et al. (2010) (see chapter 1, "Lowland Leopard Frog Reproductive Ecology") found evidence of fragmentation at the regional scale. The LLFR mtDNA data show a single dominant haplotype present at 18 (78%) of the 23 sites

distributed across the entire geographic range of the species in Arizona and northern Mexico. Alongside LLFR of this dominant haplotype, 18 less common haplotypes also occur, each with a more restricted geographic distribution. Five of these minority haplotypes (Code numbers 5, 7, 8, 9, 10), for example, occur in the upper watershed of the Bill Williams River (above Alamo Lake), at sites on Willow Creek, Trout Creek, and the Santa Maria River, and nowhere else across the study region (Oláh-Hemmings et al. 2010).

- Analyses of nuclear DNA from 512 LLFR adults from 12 sites in Arizona, many also sampled by Oláh-Hemmings et al. (2010) (Savage and Zamudio 2011, 2016; Savage et al. 2015), identified 10 genetic demes, each mostly restricted to a single tributary stream watershed even within the same river basin. For example, the LLFR sampled at the Willow Creek and Santa Maria River sites within the upper Bill Williams River watershed represent two separate genetic demes, respectively (Savage et al. 2015). Oláh-Hemmings et al. (2010) similarly found little overlap in minority haplotypes between the same two sites.

The major species accounts identify the leading causes of this fragmentation as direct habitat loss, such as stream diversions and groundwater withdrawals that eliminate surface water flow and habitat destruction by severe sedimentation; localized outbreaks of chytridiomycosis (see chapter 3, "Disease"); and the occupation of LLFR habitat by highly effective predators and/or competitors.

LLFR adults, over the course of their lifespan, must cope with at least episodically low temperatures during winter. Sredl (2018) notes that LLFR adults "… generally are inactive between November and February, [but] a detailed study of wintertime activity and habitat use has not been done." Sredl (2018) also notes that "… deep water, root masses, undercut banks, and debris piles provide … potential hibernacula."

Similarly, over the course of their lifespan, LLFR adults may need to cope with dry periods at almost any time of the year in locations that lack a permanent water source. As noted above, one study observed LLFR adults simply dispersing in response to the drying of their pond. More generally, Sredl (2018) notes: "In semipermanent aquatic systems, LLFR may survive the loss of surface water by retreating into deep mud cracks, mammal burrows, or rock fissures." Otherwise, the literature does not provide information on possible LLFR aestivation. On the other hand, the literature does note that, as with earlier life stages, LLFR adults are sensitive to elevated water salinity. In particular, Ruibal (1959 *in* Sredl 2018) found that water salinities above 6–13‰ were lethal to adult LLFR. Evaporation from a drying pool raises the salinity of the remaining water. The study by Ruibal (1959 *in* Sredl 2018) suggests that the resulting elevated salinity potentially could affect LLFR adults as much as the drying itself.

As noted above, this chapter (see "LLFR Life Stage 2 – Larvae and Juveniles"), mark-recapture studies at several LLFR sites in Arizona from 1991 to 1996 (Sredl et al. 1997a) produced estimates of both juvenile and adult survivorship at the Tule Creek site in Yavapai County, the type locality for the species (Platz 1988), and the Big Spring site in Graham County. The studies found consistently higher survivorship among adults compared to juveniles at the two sites: Adult survivorship at Tule Creek ranged from 0.04 to 3.92, while juvenile survivorship ranged from 0.08 to 2.09; adult survivorship at Big Spring ranged from 0.06 to 1.72, while juvenile survivorship ranged from 0.03 to 1.83.

As with the juveniles, adult survivorship at the Big Spring and Tule Creek sites studied by Sredl et al. (1997a) seemed to follow a seasonal pattern: higher in spring and summer, lower in fall and winter, with winter survivorship consistently the lowest. The studies at Big Spring and Tule Creek (Sredl et al. 1997a) also detected seasonal fluctuations in LLFR adult body size: SVL values were highest in April and lowest in June, with recovery strongest in October, with males appearing to grow faster than females.

As noted above, this chapter (see LLFR Life Stage 2 – Larvae and Juveniles"), the mark-recapture study by Sredl et al. (1997a) also identified an outbreak of chytrid fungus disease (see chapter 3, "Diseases") that was diagnosed only retroactively (Sredl 2018) as a cause of mortality among LLFR adults. As also noted above (see "LLFR Life Stage 2 – Larvae and Juveniles"), this outbreak of chytrid fungus disease affected juveniles more severely than it affected adults, and "[r]eduction in total habitat area due to siltation of several important pools preceded and may have exacerbated the die-off" (Sredl 2018).

Several of the major species accounts for LLFR (LCR MSCP 2016; Sredl 2018; Sredl et al. 1997a) note a lack of information concerning predation on LLFR in any life stage, as indicated above (see above, "LLFR Life Stage 2 – Larvae and Juveniles"), and identify this as a crucial gap in knowledge. The literature on LLFR includes only one formal study of predation on LLFR adults. As noted above, this chapter (see "LLFR Life Stage 2 – Larvae and Juveniles"), the study by Jones (1990 *in* Sredl 2018) found that adult and subadult black-necked garter snakes consumed adult and larval LLFR more frequently than any other prey species.

Additional evidence points to several other species as possible predators of LLFR adults in the greater LCR ecosystem. As discussed above (see "LLFR Life Stage 2 – Larvae and Juveniles"), the northern Mexican gartersnake (*Thamnophis eques megalops*) occurs along several reaches of the Bill Williams River and its main tributary above Alamo Lake, the Big Sandy River (Cotten and Grandmaison 2013; Cotten et al. 2015; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a). The USFWS and Reclamation recently added the northern Mexican gartersnake to the LCR MSCP as a covered species (USFWS and Reclamation 2018). Sabin (2018) summarizes numerous reports of this

gartersnake feeding on LLFR and other southwestern leopard frog adults; however, O'Donnell and Leavitt (2017a) note an absence of direct field observations of northern Mexican gartersnakes feeding on LLFR.

American bullfrog larvae and adults and the non-native northern crayfish are widely suspected as predators of one or more LLFR life stages (Sredl et al. 1997b), as are non-native bass and sunfish (Sredl et al. 1997b). As noted above, this chapter (see "LLFR Life Stage 2 – Larvae and Juveniles"), Cotten and Leavitt (2014) assessed the extent to which the presence of several classes of predators predicts LLFR habitat use along the LCR (Reaches 3–7), and along the Bill Williams River below Alamo Dam, and found that the presence of sunfish and largemouth bass strongly suppress LLFR numbers in this study area; otherwise, little is known about predators of LLFR adults (as noted above). The discussions of birds and mammals, fish and herpetofauna, and macroinvertebrates in chapter 4 further address possible predators of LLFR adults.

Sredl (2018) notes that LLFR adults may try to avoid predators by hiding in "… deep water, root masses, undercut banks, and debris piles …" and that

> *Adult lowland leopard frogs are cryptically colored and will sometimes remain motionless to escape detection. Other times, they rely on saltation [*to avoid predators*], escaping to deep water or shoreline cover (personal observations). Jennings and Hayes (1994a) showed a picture taken by R. Ruibal of a lowland leopard frog in a defensive posture. Although others have noted this posture, its specific purpose and effectiveness have not been investigated.*

LLFR adult growth, survival, mating, and fertility thus may depend minimally on water availability and temperatures, foraging success, predation rates, competition, disease, and the persistence of their habitat versus loss due to drying out, flood disturbance, or burial. Presumably, as aquatic organisms in a desert environment (as noted above), LLFR adult growth and survival rates also depend on their exposure to environmental contaminants and to low levels of DO as a result of water stagnation. Finally, local populations of LLFR are at risk of genetic isolation as a result of fragmentation of the drainage networks within which LLFR adults move.

Resource managers still face significant gaps in knowledge concerning all these aspects of LLFR adult life.

Chapter 3 – Critical Biological Activities and Processes

Critical biological activities and processes consist of activities in which the 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 (i.e., the rate [intensity] of these activities and processes, taken together, determine the rate of recruitment of individuals from one life stage to the next).

The LLFR conceptual ecological model identifies 12 critical biological activities and processes that affect 1 or more LLFR 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 12 critical biological activities and processes and their distribution across life stages.

Table 2.—LLFR critical biological activities and processes and their distribution among life stages
(Xs indicate life stages to which each critical biological activity applies.)

Life stage ➔ **Critical biological activity or process 🡻**	**Eggs**	**Larvae and juveniles**	**Adults**
Chemical stress	X	X	X
Competition		X	X
Disease	X	X	X
Foraging		X	X
Hybridization			X
Hydration stress	X	X	X
Mating and ovipositing			X
Mechanical stress	X	X	X
Occupancy and inter-site movement			X
Predation	X	X	X
Resting/hiding		X	X
Thermal stress	X	X	X

Except where noted, the sources for the following information are the AZGFD Heritage Data Management System Animal Abstract for LLFR (AZGFD 2006), the most recent LCR MSCP species account (LCR MSCP 2016), Platz (1988), and the online account by Sredl (2018). These publications summarize all earlier studies. Where appropriate and accessible, those earlier studies are directly cited. The identification also integrates information from both older and more recent works as well as the expert knowledge of LCR MSCP biologists. In addition, where appropriate, the discussions of individual critical biological activities and processes draw upon literature concerning leopard frogs of the Southwestern United States or larger classes of frogs in general. The following paragraphs discuss the 12 critical biological activities and processes in alphabetical order.

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. As with all frogs, LLFR in one or more life stages are vulnerable to chemical stress from several potential sources.

Freezing of the water surface during winter and warming and/or stagnation of water during hot and/or dry weather both depress the concentration of DO, potentially stressing frog eggs or larvae (Hayes and Jennings 1986; Pinder and Friet 1994; Tattersall and Ultsch 2008). However, investigators have not studied the phenomenon among LLFR. Frog egg survival and development depend in part not only on the diffusion of oxygen into the egg mass but the diffusion of metabolic wastes back out (Pinder and Friet 1994). Poor water circulation around egg masses can inhibit waste removal, but investigators have not studied the phenomenon among LLFR. As noted in chapter 2, Ruibal (1959 *in* Sredl 2018) also documents a strong sensitivity to elevated salinity in all LLFR life stages.

Amphibians worldwide—including other members of the *R. pipiens* complex—suffer deformities and altered patterns of growth, neurologic and reproductive impairment, and mortality from agricultural, industrial, and urban pollutants in the water and air that cause harm either directly or following bioaccumulation in amphibian tissue (Bank et al. 2007; Blaustein et al. 2003; Brühl et al. 2013; Davidson et al. 2002; Environmental Protection Agency [EPA] 2016; Mann et al. 2009; Smalling et al. 2015; Unrine et al. 2004;). However, the literature does not include studies of the effects of anthropogenic pollutants specifically on LLFR or other Southwestern United States members of the *R. pipiens* complex. It should also be noted that most studies of LLFR have focused on sites upstream of areas of significant agricultural, industrial, or urban land use (i.e., on sites where pollutant levels are more likely to be low). However, potential LLFR habitat occurs all along the main stem LCR valley (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014). Agricultural activities are

widespread in the valley, particularly along Reaches 4–7, and the Colorado River itself carries a diversity of pollutants (see chapters 4 and 5), including dissolved selenium, a known threat to frog reproduction (EPA 2016).

The literature also documents one possible instance of a die-off of LLFR and other Arizona leopard frogs as a result of changes in water chemistry, but in this case, the changes are due to in situ processes. Sredl et al. (1997) reports:

> *Prior to our second mark-recapture visit to Pinery Canyon in June 1994, frogs began dying at HW [Headquarters Windmill Tank]. We sampled dead and moribund frogs and water, and had both assayed for bacteria which cause red-leg. These results indicated that disease was an unlikely cause of death…. However, levels of hydrogen sulfide in the water were high enough to be toxic to aquatic wildlife…. We suspect that a high detritus load in the pond, coupled with lowering of water level, high water temperature, and low concentrations of dissolved oxygen, combined to form an anoxic environment suitable for proliferation of sulphur producing bacteria. This event reduced a population of 60–80 adult frogs to fewer than 10.*

Exposure to high levels of ultraviolet-B (UV-B) radiation can kill amphibians directly, cause sublethal effects, or exacerbate the effects of other sources of stress, and levels of UV-B radiation have been rising worldwide (Blaustein et al. 2003). However, investigators have not studied this phenomenon among LLFR.

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. As LLFR mature, they presumably become more able to avoid or remove themselves from settings in which they sense chemically unsuitable conditions—if their senses can detect these conditions and if the conditions are sufficiently localized to permit such avoidance or escape.

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. In particular, competition for food among larval amphibians and with other taxa is common in aquatic systems. For example, frog tadpoles compete with mosquitoes (Mokany and Shine 2003) and with other grazing aquatic invertebrates (Morin et al. 1988). Competition with conspecifics and other amphibians also occurs (Morin 1986; Seale 1980; Wells 2007).

As noted in chapter 2, Berven (1990) found that larger wood frog metamorphs matured sooner and were larger as adults, and these adults, in turn, had higher survival rates and higher likelihoods of mating (Howard and Kluge 1985) and

produced both larger eggs and larger clutch sizes (Berven 1982). All these consequences of larger size at metamorphosis presumably result from greater success in foraging as larvae, which is strongly affected by competition. For some frog species, the presence of other potentially competing herbivores may enhance tadpole survival. For example, Brönmark et al. (1991) observed that the grazing activity of snails increased algal productivity and, therefore, increased the food supply for *Rana temporaria* tadpoles. However, food resource competition more typically impairs the growth and development of tadpoles, potentially reducing size at metamorphosis or delaying metamorphosis, with future impacts to survival and/or reproduction as described above (Berven 1982, 1990; Howard and Kluge 1985). The literature thus does not provide clear suggestions for how competition of other species with LLFR larvae might affect this life stage, and no studies have been conducted to examine the matter.

There is even less information available about competition among adult anurans, let alone competition of adult anurans with other species. Generally, adult frogs compete for calling and oviposition sites and mates, and potentially available habitat for feeding and resting, if sites are limited. However, no studies have examined these matters for LLFR except to note the ways in which calling behaviors help maintain LLFR genetic separation from closely related species that may reproduce in the same water bodies.

Although no investigators have looked for competitive interactions affecting LLFR, larval and adult LLFR presumably do face competition from each other and from other species for both food and habitat; juvenile LLFR presumably face competition from each other and from other species for habitat. For example, LLFR larvae are generalist herbivores (see below, this chapter, "Foraging"). As a result, they may prefer or require the same food materials as other species, such as some aquatic macroinvertebrates and other small aquatic vertebrates, and therefore may face competition as they try to browse on the same kinds of organic matter. Similarly, LLFR adults may prefer the same settings for ovipositing as do other amphibians (see below, this chapter, "Hybridization," and "Mating and Ovipositing"). Chapters 4 and 6 discuss the ranges of competitors potentially facing LLFR in their larval-juvenile and adult lives. The absence of LLFR from those portions of the LCR valley now occupied by the introduced Rio Grande leopard frog (*Rana = Lithobates berlandieri*) has been identified as a potential consequence of competition between the two species, as well as a potential consequence of predation by the larger Rio Grande species on LLFR (LCR MSCP 2016). Fernandez and Rosen (1996) also report evidence that non-native crayfish reduce habitat quality for native frogs in Arizona by reducing aquatic vegetation and increasing turbidity.

Every animal species evolves strategies that permit its persistence despite such competition, including behaviors that allow it to avoid or defend against it. Avoidance behaviors may include an evolved preference for resources other than those preferred by other species in the system (resource partitioning) or an

evolved ability to switch among alternative resources as needed; however, such behaviors may not be sufficient to afford every individual LLFR full access to all necessary resources. LLFR adult males also must compete for mates, for which there are no alternative resources or options for resource partitioning. On the other hand, the literature does not mention any evidence of resource partitioning by LLFR, and evolved patterns of partitioning may not work when the competitor is an introduced species.

DISEASE

Frogs and other amphibians are subject to many viral, bacterial, and fungal diseases, as well as parasites (Duellman and Trueb 1986). Non-lethal infections may make the affected individuals vulnerable to mortality from other causes, and other sources of stress correspondingly may increase susceptibility to disease (Blaustein et al. 2003; Davidson et al. 2002).

Reviews of the decline of leopard frogs in the Western United States in general, or LLFR in particular, consistently identify disease from pathogens and parasites as likely factors (AZGFD 2006; Blaustein et al. 2003; Davidson et al. 2002; Hayes and Jennings 1986; LCR MSCP 2016; Sredl 2018). The literature contains only three reports on the incidence or effects of pathogens or parasites in LLFR.

Goldberg et al. (1998) report the results of a study of trematode (helminth) parasites in LLFR, Chiricahua leopard frogs, and American bullfrogs in Arizona; however, the study did not assess the types or magnitudes of effects LLFR may experience from this burden of infection.

Sredl et al. (1997a) report two outbreaks among LLFR of frog septicemia, commonly called "red-leg," an amphibian disease caused by the bacterium *Aeromonas hydrophila*. Hayes and Jennings (1986) identify *A. hydrophila* as a possible cause of localized extirpations of western ranid frogs but also note that "… the influence of septicemia-associated bacteria on wild ranid populations is controversial." The reports on red-leg fungal disease both document extensive illness and mortality.

A growing body of studies documents often deadly or at least debilitating infestations of chytridiomycosis (*aka* chytrid fungal disease) and its agent, *Batrachochytrium dendrobatidis* (*aka Bd*), in LLFR and closely related species (see Bradley et al. 2002; Jaeger et al. 2016, 2017; Rosen et al. 2013; Savage and Zamudio 2011, 2016; Savage et al. 2015; and see discussions in LCR MSCP 2016 and Sredl 2018). However, chytridiomycosis causes mortality among LLFR only in winter and only in some populations and in some genetic demes within these

populations (Bradley et al. 2002; Savage and Zamudio 2011, 2016; Savage et al. 2015). The effects of chytridiomycosis among LLFR thus vary depending on the interplay of genetic, environmental, and demographic factors (Savage et al. 2015).

The studies of *Bd* have chronicled a history of high mortality among LLFR range-wide from this introduced disease beginning in the 1990s. Fortunately, the studies of *Bd* among LLFR and closely related species, particularly the relict leopard frog, have also identified two positive trends. First, *Bd* infectious abilities decline significantly above 25 °C and even more severely above 28 °C (Bradley et al. 2002; Jaeger et al. 2016, 2017; Savage et al. 2015). Outbreaks among leopard frogs of the Southwestern United States occur overwhelmingly during cold winter weather, and populations in geothermal springs with warm temperatures year round appear unaffected (Bradley et al. 2002; Jaeger et al. 2016; LCR MSCP 2016; Rosen et al. 2013; Savage et al. 2015; Sredl 2018). Second, LLFR and closely related species appear to have rapidly evolved a genetically based tolerance to *Bd* (Jaeger et al. 2017; Savage and Zamudio 2011, 2016; Savage et al. 2015). Tolerant individuals remain unaffected by an infection or clear themselves of infection. This evolution of tolerance has occurred over a timespan of perhaps only two decades in multiple local LLFR populations in Arizona that lack opportunities for genetic exchange. As discussed in chapter 2 (see "LLFR Life Stage 3 – Adults"), investigators have found evidence that outbreaks of chytridiomycosis among LLFR may both promote and be promoted by local genetic isolation (Savage and Zamudio 2011, 2016; Savage et al. 2015).

FORAGING

LLFR larvae and adults must find and acquire food to survive. Foraging success also likely affects LLFR reproductive output (fecundity): Among anurans in general, larger females typically produce larger clutches (Duellman and Trueb 1986).

LLFR larvae begin foraging immediately after emerging from their eggs but completely stop during the final (juvenile) phase of their metamorphosis. As noted in chapter 2, the literature describes LLFR larvae as herbivores, feeding specifically on algae, organic debris, plant tissue, and micro-organisms. However, except for brief comments by Sartorius and Rosen (2000), discussed below, all published descriptions of LLFR larval foraging in fact refer to only a single, unpublished report from southeastern Arizona (Marti and Fisher 1998). Sartorius and Rosen (2000) describe LLFR larvae feeding on filamentous algae (*Cladophora*) mats and small organisms within them, and they also note a possible seasonal factor in foraging success: Larvae that hatch in September or October "… face lower temperatures and reduced primary productivity, which prolong larval development and extend exposure to predation, fall and winter drought, and cold floods in late winter." The literature reviewed for this CEM

does not record any other studies of feeding behavior or diet among LLFR larvae. Sredl (2018) identifies this as a significant gap in knowledge of the species.

The same unpublished paper that serves as the main reference work on LLFR larval foraging is also the only source of information about larval foraging by the closely related Chiricahua leopard frog. Otherwise, the literature on Chiricahua leopard larvae might have provided hints about the possible diet of larval LLFR. As noted in chapter 2, LLFR were at one time classified as the lowland variant of a larger complex of leopard frogs, of which the well-studied northern leopard frog is the most common member. Northern leopard frog larvae are herbivorous, feeding "… on attached and suspended algae, other attached plant and animal material, and occasionally on dead animals" (Rorabaugh 2018a).

As also noted in chapter 2, LLFR adults are carnivores, consuming arthropods and other invertebrates, including beetles, flies, terrestrial stages of aquatic invertebrates, spiders, earthworms, slugs, and snails (Degenhardt et al. 1996 *in* AZGFD 2006; Sredl 2018; Stebbins 1951; Stebbins 1985 *in* AZGFD 2006). LLFR adults may also cannibalize LLFR larvae (see chapter 2). AZGFD (2006) also notes that "Stomach analyses of other [adult] members of the leopard frog complex from the western United States show a wide variety of prey items, including many types of aquatic and terrestrial invertebrates (e.g., snails, spiders, insects) and vertebrates (e.g., fish, other anurans [including conspecifics], small birds)." However, the literature review for the present CEM did not identify any studies that specifically investigated diet or foraging behaviors among LLFR adults (LCR MSCP 2016).

HYBRIDIZATION

Hybridization occurs when two species together produce live offspring that share genetic materials from both parental species. A review by Scribner et al. (2001) identifies several factors that elevate the potential for hybridization among closely related fish species in their natural ranges, which also apply to amphibians (Frost and Platz 1983; Platz and Frost 1984): External fertilization; weak behavioral isolating mechanisms, including overlapping breeding seasons and habitat; competition for limited breeding habitat; unequal abundance of the two parental species; and trends of decreasing habitat complexity.

LLFR is sympatric with the closely related Chiricahua leopard frog at elevations of 1180–1700 m at a few sites in central and southeastern Arizona (LCR MSCP 2016), and the two species occasionally hybridize in these areas (Frost and Platz 1983; Platz 1988; Platz and Frost 1984; Stebbins 2003 in AZGFD 2006). Laboratory studies (Frost and Platz 1983) indicate that the two species are genetically compatible, producing developmentally normal hybrid embryos in the first generation. However, Frost and Platz (Frost and Platz 1983; Platz and

Frost 1984) found only a small (3%) incidence of first-generation hybrids in the field and no backcross individuals. They conclude that behavioral differences, particularly differences in mating calls, maintain the genetic separation of the two species in their natural areas of sympatry (also see Sartorius and Rosen 2000) and that the apparent inability of lowland-Chiricahua first-generation hybrids to produce viable backcrosses also helps maintain this genetic separation.

The Chiricahua leopard frog does not naturally occur within the greater LCR ecosystem and, therefore, does not pose a risk of hybridization along the LCR. No studies have been conducted to examine the potential for hybridization between LLFR and the introduced Rio Grande leopard frog, which occurs in LCR Reaches 6 and 7, as noted in chapter 2. LLFR and the closely related relict leopard frog are not sympatric anywhere in their individual ranges (Oláh-Hemmings et al. 2010).

HYDRATION STRESS

Dehydration causes physiological stress and mortality among frog species in general. Frog eggs and larvae must remain immersed to survive and have no means for relocating themselves when their habitat dries out; frog juveniles (metamorphs) have only very limited capabilities to do so. Adults can survive out of water for some length of time and, when their habitat dries, may try to move to another site or may seek refuge underground. Some frog species can remain underground for prolonged dry periods through aestivation (see below, this chapter, "Resting/Hiding"). Some frogs also reduce water loss by avoiding activity during the hottest times of the day (Stebbins and Cohen 1995).

The literature on LLFR does not include any formal studies of adaptations to risks of dehydration, but it does include anecdotal studies. As noted in chapter 2, Sartorius and Rosen (2000) observed mortality of LLFR eggs only among those near the tops of masses that became exposed to air. The literature does not include any studies of possible aestivation among LLFR (Sredl 2018). Howland et al. (1997) state that, "Unlike many other anurans of the desert southwest, leopard frogs are obligate wetland species …. They lack adaptations that allow others to endure long periods of drought." However, LLFR adults appear to exhibit at least three behavioral adaptations to avoid dehydration. First, LLFR exclusively use locations with permanent or nearly permanent surface water and never use fast-drying ephemeral pools for breeding (O'Donnell and Leavitt 2017a, 2017b). Second, Howland et al. (1997) report finding LLFR adults in shallow mud cracks and cattle hoof prints in cattle tanks undergoing drying and suggest that LLFR may hide in deeper mud cracks, mammal burrows, and similar underground microhabitats during episodes of complete drying. (A brief review by Pelinson et al. (2016) suggests that anurans may readily use puddles in cattle hoof prints as aquatic refuge and stepping-stone habitat—see chapter 4, "Birds

and Mammals"). Third, LLFR also may attempt to relocate away from drying habitat. As noted below (see below, this chapter, "Occupancy and Inter-Site Movement"), Sredl et al. (1997a) specifically recorded adult LLFR dispersal both up- and down-drainage from a pond undergoing drying. However, LLFR adults can survive through dispersal only if drying conditions are localized and other wet habitat is available nearby. Zylstra et al. (2015) analyzed data on 95 unique adult LLFR observed and resighted at least once during a mark-resight study in the Rincon Mountains in Saguaro National Park. The data identify 129 movements between pool complexes over distances of 5–272 m (mean = 63.6 ± 4.68), all of which occurred exclusively along stream courses. Howland et al. (1997) report evidence of "… a local extinction event throughout the study area, caused, at least in part, by drying of nearly all available aquatic habitat in an unusually dry year."

MATING AND OVIPOSITING

Mating and ovipositing are two phases of a single process of frog reproduction: Prospective mates find and select each other at an aquatic breeding location selected by one or both participants, with the timing of this event cued by environmental factors. With LLFR, as with most ranid frogs, the female then deposits her eggs in the water in a single mass attached to vegetation or some other solid matter, while the male, mounted on the back of the female (*aka* amplexus), fertilizes the eggs externally as they emerge (Duellman and Trueb 1986; Stebbins and Cohen 1995; Wells 2007 and references therein).

As noted in chapter 2, the literature reviewed for the present CEM does not provide firm evidence concerning the factors that may cue LLFR mating, and in fact, it explicitly notes the absence of investigations on the subject. The literature does offer suggestions for such cues for LLFR and related species in the Southwest, focusing on rainfall and changes in air and/or water temperature. The results of the study by Sartorius and Rosen (2000), in particular, appear to indicate that changes in air and/or water temperature are salient and that LLFR may mate simply when water temperatures allow, particularly in geothermal springs, regardless of whether rainfall has occurred recently or not (see chapter 2).

The literature also does not indicate whether LLFR adults move between sites to breed. As noted in chapter 2, LLFR do not appear to participate in breeding migrations, a type of collective behavior in some amphibians (Sredl 2018). On the other hand, individual LLFR adults do move between localities, as discussed below, this chapter ("Occupancy and Inter-Site Movement"). However, the literature does not suggest that such inter-site movement occurs particularly for purposes of mating; rather, the literature suggests that such movements occur in

response to degrading habitat conditions that drive adults away from their natal site. As noted above, the reasons for such movements among LLFR have not received formal investigation.

Adult frogs, in general, develop their stores of mature gametes for each breeding season over a span of weeks to months, cued by photoperiod and temperature, during which time they also undergo changes in hormonal biology (Gilbert 2000). However, no studies have been conducted to investigate sexual maturation and readiness for mating in LLFR in particular.

According to Platz and Frost (1984), LLFR adult males attract a potential mate by emitting a distinctive mating call; however, no studies have been conducted to investigate any other details of mating behavior among LLFR. Among ranid frogs in general, males typically select their calling sites, and females typically move away to a different but nearby oviposition site after selecting a mate (Wells 2007).

LLFR breed in a wide variety of both artificial and natural mesohabitat settings (see chapter 4), resulting in their categorization by all species accounts as habitat generalists for reproduction. Sredl (2018) describes LLFR breeding sites as follows:

> *Natural systems include rivers, permanent streams, permanent pools in intermittent streams, beaver ponds, cienegas (= wetlands), and springs; while manmade systems include earthen cattle tanks, livestock drinkers, canals, irrigation sloughs, wells, mine adits, abandoned swimming pools, and ornamental backyard ponds…. The preponderance of historical localities are small to medium-sized streams and rivers.*

Within these mesohabitats, however, LLFR show a high level of selectivity in microhabitat conditions for ovipositing. Microhabitat conditions of particular importance include temperature, salinity, water depth, the availability of particular aquatic vegetation or substrate materials for attaching the egg mass near the water surface at the right relative depth, the proximity of locations onto which juveniles can crawl out of the water, and the density and composition of canopy vegetation (AZGFD 2006; Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; LCR MSCP 2016; Leavitt et al. 2017; Miller and Cotten 2016; Sartorius and Rosen 2000; Sredl 2018). Sredl (2018) further notes:

> *In lotic habitats, [*egg masses*] are concentrated at springs, near debris piles, at heads of pools, and near deep pools associated with root masses …. The constant flow and warm water temperature of thermal springs, which permit year-round adult activity and winter breeding, and depauperate fish communities make these sites particularly important breeding habitat for leopard frogs in New Mexico.*

The literature also consistently mentions but does not quantify a preference for breeding in water with low flow velocities or other forms of circulation (i.e., in water that is neither stagnant nor fast-flowing). Chapter 4 discusses LLFR microhabitat preferences for breeding more fully as habitat elements in this CEM.

Field surveys for LLFR routinely count the number of egg masses encountered (AZGFD 2006; Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; LCR MSCP 2016; Leavitt et al. 2017; Miller and Cotten 2016; O'Donnell and Leavitt 2017a, 2017b; Sartorius and Rosen 2000; Sredl 2018). However, only one study reported on even the relative sizes of LLFR egg masses—Sartorius and Rosen (2000) report that eggs deposited early in the spring breeding season were about twice the size of those deposited later in the same season—and no studies report the absolute number of LLFR eggs in any masses encountered. As a result, the literature provides no quantitative data on LLFR fecundity or fertility, let alone on how these may vary with other factors such as female size or health. The literature also does not indicate the number of times an individual female may breed in any single year or what factors may affect that number at a given location—additional longstanding gaps in knowledge (Platz 1988).

Among anurans in general, as noted above, this chapter (see "Foraging") and chapter 2, larger (but not aged) and/or healthier females typically produce larger clutches (Duellman and Trueb 1986; Stebbins and Cohen 1995). According to Stebbins and Cohen (1995), clutch size depends in part on genetics, nutritional condition of females, number of repetitive breedings, and the temperature and length of the growing season, among other factors.

For comparison, Rorabaugh (2018a) reports that the related species, the northern leopard frog, produces clutches with 645–7,648 eggs, and Sredl and Jennings (2018) report that the Chiricahua leopard frog produce clutches with 300–1,485 eggs. McGinley (1989) mentions several ways in which larger clutch sizes increase the probability of frog embryo survival to hatching: Larger clutch sizes may reduce the chances that predators, pathogens, or parasites will damage or consume all eggs in a clutch, allowing more to survive, and may reduce the chances of desiccation affecting all eggs "due to lower surface/volume ratios or a more stable thermal environment." Sartorius and Rosen (2000) report that LLFR mortality was low within egg masses, and that this mortality usually occurred near the top of the mass, among eggs that were at least occasionally exposed to the air.

MECHANICAL STRESS

LLFR in every life stage may suffer stress and outright physical destruction due to mechanical impacts, abrasions, and burial. LLFR in the LCR valley and its tributaries presumably may encounter many situations that could result in

mechanical stress, including encounters with human foot traffic and vehicles; entrainment by inescapable flow velocities and turbulence, such as along high-volume diversion or irrigation ditches; burial by a rapid influx of sediment; unsuccessful predator attacks; or capture during monitoring.

Mechanical stress that does not result in mortality nevertheless may leave the affected individuals more vulnerable to infections and mortality from other causes. LLFR adults may try to avoid or escape settings where they detect mechanically hazardous conditions—if these conditions are sufficiently localized to permit such avoidance or escape. Alternatively, LLFR adults may seek refuge habitat in such settings (see below, this chapter, and chapter 2). LLFR eggs, larvae, and juveniles can avoid disturbances only on a more limited spatial scale in their immediate vicinity.

All amphibians face risks of stress and outright physical destruction due to mechanical impacts, abrasions, and, sometimes, burial. However, the literature contains only one unambiguous record of mechanical stress leading to mortality among LLFR, along with two other more ambiguous records:

- Sartorius and Rosen (2000) describe the cause of failure of 2 egg masses among 58 studied as follows: "The two egg masses that did not survive had been deposited near hiking trail stream-crossings and were detached from their deposition sites (possibly by hikers or their pets) and were later located downstream. The egg masses were partially disarticulated and presumed to have been destroyed as they continued downstream."

- As noted in chapter 2, the mark-recapture study by Sredl et al. (1997a) identified a significant flood event and losses of habitat area due to siltation as possible causes of, or contributors to, extirpations of LLFR at six pools studied over a period of 2 years. However, the study did not directly document these causal relationships but only inferred them from the data on changes in LLFR abundance in relationship to the flooding and siltation events.

- Parker (2006) describes the destruction of LLFR habitat by floods following intense rainfall events that carried in large volumes of ash, gravel, and coarse sand into ephemeral stream channels in the Rincon Mountains in Saguaro National Park following wildfires. The debris carried in by the floods buried pools previously occupied by LLFR along these washes, resulting in local extirpation. However, the study did not determine whether the burial events directly caused any mortality. LLFR adults can move to new habitat sites and, as Sartorius and Rosen (2000) have noted, the timing of LLFR reproduction greatly reduces the chances of LLFR eggs and larvae being harmed by summer monsoon storms and their associated intense flooding and scouring events.

LLFR are likely highly adapted to the highly variable hydrology of their native range, including the likelihood of habitat-altering flood pulses (see chapter 1, "Lowland Leopard from Reproductive Ecology"). For example, LLFR have long resided in the Bill Williams River, including below Alamo Dam, where the river exceeded 500 cubic meters per second (m^3/s) (17,655 cubic feet per second [ft^3/s]) seven times between 1940 and the completion of the dam in 1968 (Shafroth et al. 2010). Controlled releases from the dam in 2004–05, 2006, 2007, and 2008 reached peak discharges of 150–204 m^3/s, 69 m^3/s (for 48 hours), 29 m^3/s (for 16 hours), and 65 m^3/s (for 8 hours), respectively (5,297–7,203 ft^3/s, 2,436 ft^3/s, 1,024 ft^3/s, and 2,295 ft^3/s, respectively (Andersen et al. 2011; Shafroth et al. 2010;). These controlled releases, substantially smaller than the pre-dam flood pulses, also failed to dislodge LLFR from the lower river (Cotten 2011). Sredl et al. (1997a) in fact propose that flood disturbances may benefit overall LLFR abundance: A population increase occurred following a major scouring flood at the Tule Creek study site, Arizona, that cleared sediment and vegetation from previously more extensive open water habitats.

OCCUPANCY AND INTER-SITE MOVEMENT

LLFR occupy only locations with standing or flowing water present either permanently (perennially) or during at least the spring breeding season (Sartorius and Rosen 2000; Sredl et al. 1997a; Swann and Wallace 2010; Wallace et al. 2010) (see chapter 4, "Hydrologic Regime"). Other factors, including the composition and densities of woody and herbaceous vegetation, also affect the likelihood that LLFR will occupy an individual site (see chapter 4, "Herbaceous Vegetation" and "Woody Vegetation"). LLFR persist at hydrologically and vegetatively suitable locations, unless some catastrophic condition intervenes, and readily reoccupy sites following a catastrophe if suitable hydrologic conditions are present. Catastrophes mentioned in the literature that could lead to a local disappearance of LLFR include disease (see above, this chapter, "Disease"), filling of a site by sediment following a flood (see chapter 4, "Substrate"), and competitive exclusion or predation by non-native sunfish, largemouth bass, crayfish, American bullfrogs, and/or Rio Grande leopard frogs (see above, this chapter, "Competition" and "Predation").

Inter-site movement is a negative corollary of site occupancy. As noted in chapter 2, LLFR adults sometimes leave their natal sites and move to other sites. Presumably, departures of individual LLFR from a natal site need not be part of a complete abandonment of the natal site: the sites to which these adults move may already be occupied by LLFR, and LLFR adults from two or more sites may colonize the same previously unoccupied site. By bringing together adults from different natal sites, such movements ensure the mixing of gene variants within and between local populations (i.e., ensure gene flow). As discussed in chapter 1, "LLFR Life Stage 3 – Adults," several studies have proposed that drainage

network fragmentation (loss of connectivity), preventing adult movement between populations, has resulted in significant genetic isolation among local populations of LLFR within and between watersheds throughout its range (Goldberg et al. 2004 *in* LCR MSCP 2016; Oláh-Hemmings et al. 2010; Rosen et al. 2013; Savage et al. 2015).

Only a few studies have been conducted to investigate LLFR inter-site movement or the factors that may trigger it:

- Sredl et al. (1997a) studied LLFR movement following drying of a pond. The study recorded 154 frogs that moved approximately 250 m upstream to a pond that did not dry and 4 frogs that moved 900 m downstream. Howland et al. (1997) report finding LLFR at a cattle watering tank "up a steep narrow drainage [approximately] 1.0 air mile from the nearest known perennial water" as further evidence of the ability of LLFR to move between sites.

- As noted in chapter 1, "LLFR Life Stage 3 – Adults," investigations of LLFR in the Rincon Mountains in Saguaro National Park by Goldberg et al. (2004 *in* LCR MSCP 2016) found that local populations were genetically much more closely related within versus between drainages. The investigators interpreted these results to indicate that LLFR adult movement between local populations occurs at least mostly within drainages and not along straight lines. However, the study by Goldberg et al. (2004 *in* LCR MSCP 2016) did not assess movement distances or timing.

- Witte et al. (2008) used an AZGFD database of ranid frog historic and current occurrences to assess factors that might be associated with (statistically predictive of) local disappearances of native ranid frogs in Arizona, including LLFR. The study found that the odds of ranid frogs disappearing from an individual site were significantly greater if they had also disappeared from another site within 6 kilometers (km), eliminating nearby sources for recolonization, and correspondingly were significantly less if ranid frogs had not also disappeared from another site within 4 km. The study distinguished sites based on their proximity in air miles rather in terms of distance within drainage networks.

- As noted above, this chapter (see "Hydration Stress"), Zylstra et al. (2015) analyzed data on adult LLFR observed and resighted at least once during a mark-resight study in 2013 in the Rincon Mountains in Saguaro National Park. The study marked 105 unique adult frogs between May and December 2013 and resighted 95 (90%) at least once. The resightings identified 129 movements between pool complexes over distances of 5–272 m (mean = 63.6 ± 4.68), all of which occurred exclusively along

> stream courses. Each pool complex consisted of closely adjacent pools that functioned as integrated habitat because of their close proximity (< 120 m separation when surface water was not present outside of the surveyed pools). Seven (5%) of the 129 movements occurred between complexes, including 1 that occurred when there was no surface water between the 2 pool complexes (Zylstra et al. 2015).

Hinderer et al. (2017) studied inter-site movement and its triggers in the related, partially sympatric Chiricahua leopard frog. Their study used radio tracking to assess inter-site movement between livestock watering tanks in a single stream valley. They found that the frogs moved more during rainfall events of low to moderate magnitude than they did during times of high or no rainfall. Movement did not correlate with changes in water temperature. Those frogs that moved traveled an average of 97 meters per day, including one individual that traveled nearly 10 km over a period of 36 days. Neither the timing nor the distances traveled varied statistically with the sex or size of the individuals. Unfortunately, it is not possible at the present time to compare the findings by Hinderer et al. (2017) for the Chiricahua leopard frog with any findings for LLFR. The species are genetically close and can form at least first-generation hybrids (see below, this chapter,), but have different breeding phenologies (Sartorius and Rosen 2000) that could affect their patterns of inter-site movement. On the other hand, the study by Hinderer et al. (2017) at least suggests methods that could be used to study the topic in LLFR.

PREDATION

LLFR experience injury and mortality due to predation during every life stage, as do all wild animals. Every animal species has evolved strategies that permit its persistence despite predation, including specific behaviors, body features, or reproductive strategies that allow it to avoid, escape, defend against, or counterbalance losses from predation. As noted in chapter 1, for example, a tendency to high fertility and wide-ranging movement between sites within drainage networks historically may have helped LLFR in its natural settings counter the effects of predation pressure; however, such strategies may not work as well against predation by non-native species.

Among frogs in general, predation pressure is highest on their eggs and larvae (Duellman and Trueb 1986). Predators of frog eggs include aquatic invertebrates and fishes, and even other amphibians such as green frogs (Petranka and Kennedy 1999). Predators of tadpoles include aquatic invertebrates such as odonates (dragonflies and damselflies), Dytiscids (predacious diving beetles), and crayfish; various fish species; other amphibians such as stream salamanders or bullfrogs; reptiles such as snakes and turtles; birds such as bitterns and herons; and small

mammals. A wide array of vertebrates, including fishes, larger frogs, snakes, and wading birds prey on adult frogs (Duellman and Trueb 1986; Wells 2007 and references therein).

As noted in chapter 2, several of the major species accounts for LLFR (LCR MSCP 2016; Sredl 2018; Sredl et al. 1997a) explicitly note a lack of information concerning predation specifically on LLFR in any life stage and identify this as a crucial gap in knowledge. The sections of chapter 2 on each life stage identify all species known or strongly suspected to prey on LLFR in each life stage: the non-native virile or northern crayfish for LLFR eggs; northern crayfish, black-necked gartersnake, northern Mexican gartersnake, American bullfrog, black bullhead, channel catfish, green sunfish, bluegill, largemouth bass, flathead catfish, and redbelly tilapia for LLFR larvae and juveniles; and black-necked gartersnake, northern Mexican gartersnake, and American bullfrog, for LLFR adults. The native Yuma clapper rail (*Rallus longirostris yumanensis*) and least bittern (*Ixobrychus exilis*), and the non-native Rio Grande leopard frog all occur in the greater LCR ecosystem and are known to consume larval and adult frogs, including other leopard frogs, and therefore are suspected to consume larval and adult LLFR as well. The discussions of birds and mammals, fish and herpetofauna, and macroinvertebrates in chapter 4 further address possible predators of LLFR in any life stage.

LLFR historically were widely and continuously distributed and abundant wherever suitable physical habitat occurred (AZGFD 2006; LCR MSCP 2016; Sredl 2018). This widespread distribution presumably indicates an absence of native predators capable of eliminating LLFR for very long in any one locality or larger area. In contrast, the patchy distribution of LLFR that exists today is thought to result in part from predation by one or more non-native species resulting in numerous local extirpations (Sartorius and Rosen 2000). Hayes and Jennings (1986) note an inverse relationship between the abundances of Western United States ranid frog species and non-native aquatic predators in general, which they attribute primarily to the direct effects of non-native predation. Gamradt and Kats (1996) found evidence that the presence of non-native crayfish at a site may also deter amphibian breeding.

Hayes and Jennings (1986) also note that native ranid frogs of the Western United States in general may lack defensive adaptations such as unpalatability that non-native species such as the American bullfrog may possess. Interactions among predators themselves may further exacerbate the challenges facing LLFR from both native and non-native predators: Sartorius and Rosen (2000) note that "… Centrarchid fishes may alter the composition of anuran communities by avoiding bullfrog tadpoles and feeding on competitor and predator species."

Efforts to restore LLFR or related leopard frogs to individual sites typically include removal of non-natives such as the American bullfrog, northern crayfish, and red swamp crayfish (*Procambarus clarkii*) (AZGFD 2006; Rosen et al. 2013;

Sredl 2018). When such efforts fail to achieve complete removal, LLFR restoration typically fails (Rosen et al. 2013). On the other hand, LLFR do well in locations where environmental factors, such as the occurrence of flood pulses from intense summer rainfall, help control the presence or abundance of non-natives such as the American bullfrog (Rosen et al. 2013; Sartorius and Rosen 2000; also see chapter 4, "Hydrologic Regime"). Unfortunately, no data are available on actual predation rates on LLFR in any life stage in natural settings.

The literature notes other possibilities for LLFR adaptations to predation. Sredl (2018) states:

> *Adult lowland leopard frogs are cryptically colored and will sometimes remain motionless to escape detection. Other times, they rely on saltation, escaping to deep water or shoreline cover (personal observations). Jennings and Hayes (1994a) showed a picture taken by R. Ruibal of a lowland leopard frog in a defensive posture. Although others have noted this posture, its specific purpose and effectiveness have not been investigated.*

In turn, Hayes and Jennings (1986) state, with reference to the predation ecology of native ranid frogs in California, possible analogs for LLFR predation ecology:

> *Native California predatory fish feed primarily by sight on prey in the water column or on organisms exposed on accessible surfaces, only infrequently disturbing aquatic vegetation or benthic sediment…. This mode of feeding allows some benthos-dwelling organisms, such as tadpoles, to avoid predation because they are rarely exposed.*

Frog larvae may alter their behavior in the presence of predators (Alford 1999; Wells 2007 and references therein), with potential bioenergetic consequences. For example, they may alter microhabitat use, as do common spring peeper (*Hyla = Pseudacris crucifer*) (Morin 1986); form schools, a safety-in-numbers strategy used by *Bufo bufo* (Watt et al. 1997); and/or reduce feeding activity and seek refuge (Lawler 1989). This latter behavior has been shown in bullfrogs, where reduced foraging activity in the presence of dragonfly naiads resulted in a reduced growth rate (Werner and Anholt 1996). However, the intensity of the effect among bullfrogs was mediated by the size of the tadpoles, with larger bullfrog tadpoles remaining more active (Werner and Anholt 1996). Similarly, American toads reduced foraging activity in the presence of predators, resulting in smaller size at metamorphosis (Skelly and Werner 1990). Kiesecker and Blaustein (1998) observed that red-legged frogs (*Rana aurora)* experienced decreased mass at metamorphosis and a longer larval period when exposed to predatory fishes and dragonflies. A smaller size at metamorphosis may negatively affect future survival and reproductive success in amphibians (Berven 1990; Scott 1994). Sosa et al. (2009) found that, in a microcosm study in the presence of non-native green sunfish, LLFR larvae become 90% less active than in control tanks without fish predators. Such changes in behavior potentially have

bioenergetics costs because of the energy required for avoidance behaviors and/or lowered food intake among frogs that reduce their feeding activities in the presence of predators. No investigators have studied the bioenergetics of LLFR predator avoidance.

Frog larvae also may undergo changes in body shape and color patterns (induced morphological changes) in the presence of predators (Van Buskirk et al. 1997). In the microcosm study with green sunfish noted above, Sosa et al. (2009) also found that the LLFR larvae exposed to green sunfish exhibited changes particularly in tail shape that the investigators thought might confer greater swimming speed. Unfortunately, these morphological changes did not confer greater survivability to the LLFR larvae in the study.

RESTING/HIDING

LLFR larvae-juveniles and adults have distinct repertoires of behaviors for resting and shielding themselves from visibility and exposure to potentially threatening environmental conditions. LLFR larvae-juveniles rest and hide exclusively in the water. The literature otherwise provides little information on resting/hiding behaviors among LLFR larvae-juveniles; however, as with most frog tadpoles, LLFR larvae presumably scatter when startled and, when not actively swimming or foraging, keep themselves from drifting in the water by simply settling themselves to the bottom in shallow settings with very low flow or resting in vegetation. Hayes and Jennings (1986) note that the larvae of native ranid frogs in California—a possible analog for LLFR—"… use benthic sediment, aquatic vegetation, or rocky crevices as refuges." As noted above, this chapter (see "Predation"), frog larvae also may undergo changes in body shape and color patterns (induced morphological changes) in the presence of predators (Van Buskirk et al. 1997) presumably to reduce their visibility.

LLFR adults rest and hide in the water, along the shore and on dry land immediately around their aquatic and wetland sites, and underground. As discussed above (see above, this chapter, "Hydration Stress"), Howland et al. (1997) observed LLFR adults in shallow mud cracks and cattle hoof prints in cattle tanks undergoing drying and suggest that LLFR may hide in deeper mud cracks, mammal burrows, and similar underground microhabitats during episodes of complete drying. It apparently is not unusual for anurans to use cattle hoof prints as aquatic refuge and stepping-stone habitat (Pelinson et al. 2016)—also see chapter 4, "Birds and Mammals"). They also may attempt to leave drying sites altogether (see above, this chapter, "Occupancy and Inter-Site Movement").

The literature consistently indicates that LLFR adults rest, hide, and breed in settings with specific microhabitat characteristics within their individual aquatic-wetland home sites (see details in chapter 4). Surveys by the AZGFD on behalf

of the LCR MSCP along the LCR and in the Bill Williams River watershed statistically demonstrate that LLFR select locations for resting and breeding with greater aquatic vegetative cover immediately overhead and greater canopy cover along the nearest shoreline, compared to average conditions at these aquatic-wetland sites (Cotten and Leavitt 2014; Leavitt et al. 2017; also see chapter 4, "Herbaceous Vegetation" and "Woody Vegetation"). These findings confirm anecdotal records that LLFR preferentially select microhabitats for resting and breeding with emergent aquatic vegetative cover and nearby littoral canopy cover (AZGFD 2006; Sredl 2018; Swann and Wallace 2010). The relict leopard frog has a similar pattern of habitat selection for resting and breeding, but it prefers more open habitat with less herbaceous or woody vegetation cover (Bradford et al. 2004, 2005; Harris 2006; Jaeger et al. 2010, 2014). Hayes and Jennings (1986) note that removal of riparian cover is often cited as an important cause of the disappearance of ranid frogs across the Western United States in general. AZGFD (2006), Cotten (2011), Cotten and Grandmaison (2013), Cotten and Leavitt (2014), Sredl (2018), and Swann and Wallace (2010) also mention adult LLFR hiding in deep water, holes and cracks in rock substrates, root cavities, and debris piles; below undercut banks; under logs, rocks, and ledges; and within submergent vegetation.

LLFR adults may also vary their activity levels between daytime and nighttime hours. The AZGFD surveyors conducted several types of survey methods—visual encounter surveys (VESs), funnel trap arrays, and digital automated recorders (DARs)—during both daytime and nighttime hours along the LCR and in Bill Williams River watershed (O'Donnell and Leavitt 2017a). The authors note that funnel trap arrays "… have the ability to capture individuals at all hours of the day. They can be present during high activity times that might be missed by other methods. Generally, VESs are conducted during the night because LLFR are easier to detect then, but that may not be when they are most active." However, the AZGFD has not yet published analyses of the timing of LLFR detections resulting from these surveys, and no other studies document the timing of LLFR activity versus inactivity (resting) between daytime and nighttime hours.

THERMAL STRESS

Exposure to air or water temperatures outside their ranges of tolerance presumably render LLFR in every life stage vulnerable to reduced metabolic rates, reduced growth, impaired performance, disease, stress, and mortality, as is the case with all frogs (Wells 2007 and references therein). Mann et al. (2009) summarize evidence for synergistic effects of thermal stress with disease and chemical stress and summarizes studies indicating that "… several amphibian species are masculinized by high temperatures or feminized by low temperatures during larval life and manifested as distorted sex ratios obtained at or soon after metamorphosis." As noted in chapter 1 (see "Lowland Leopard Frog Reproductive Ecology"), Zweifel (1968) suggests that the rate of maturation of

LLFR eggs likely varies with water temperature based on data for closely related species in the region. Findings from a study of the relict leopard frog (Goldstein et al. 2017) similarly suggest that the rates of maturation and survival of LLFR larvae to metamorphosis likely also vary with water temperature, with thermal stress in extreme water temperatures (15 and 35°C) slowing or stopping maturation and/or resulting in higher (up to 100%) mortality. Goldstein et al. (2017) specifically found that, among relict frog larvae raised in water at 15, 20, 25, 30, and 35 °C, "development was arrested in the 15 °C group, and survivorship declined to 64% after 191 days… Survivorship of the 20, 25, and 30 °C acclimation groups was 82, 94, and 66%, respectively, whereas none survived at 35 °C. The time to metamorphosis was significantly shorter for the 25 °C group (67 ± 1 days), followed by the 30 °C (98 ± 2 days) and 20 °C (264 ± 7 days) groups."

Once LLFR become adults, they presumably become more able to avoid or remove themselves from settings in which they sense thermally unsuitable conditions—if the conditions are sufficiently localized to permit such avoidance or escape. However, LLFR that seek deeper water in which to find cooler temperatures or simply to hide (see above, this chapter, "Resting/Hiding") during the summer months could encounter lower concentrations of DO in these same settings (Sredl et al. 1997a; also see above, this chapter, "Chemical Stress"). Water temperature also interacts synergistically with at least two infectious agents that affect LLFR: LLFR show greater susceptibility to red-leg and *Bd* at colder temperatures (Blaustein et al. 2003; Sredl et al. 1997a; also see above, this chapter, "Disease"), while warm water can be used as a treatment to help LLFR avoid or recover from *Bd* infection (Rosen et al. 2013; Savage et al. 2015).

Chapter 4 discusses the available evidence on LLFR thermal preferences and tolerances. The literature mostly does not document the effects of thermal stress per se but rather mostly documents LLFR behavioral responses to potentially thermally stressful conditions. Sartorius and Rosen (2000) recorded LLFR eggs hatching in the wild in 15–18 days but did not record whether the time to hatching varied with temperature. LLFR larvae that hatch in spring can metamorphose in 3–4 months, while those that hatch in fall may require up to 9 months, with the longer time to metamorphosis coinciding with their overwintering in colder weather (Sredl 2018). Sartorius and Rosen (2000) note that larvae hatched in fall "… face lower temperatures and reduced primary productivity, which prolong larval development and extend exposure to predation, fall and winter drought, and cold floods in late winter." The literature also consistently notes that LLFR become less active with increasing cold in winter—except in geothermal springs—and increasing heat in summer (Howland et al. 1997). The cover-seeking behavior observed consistently among LLFR (see above, this chapter, "Resting/Hiding") also could help protect LLFR adults from the heat of summer weather.

Chapter 4 – Habitat Elements

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

This chapter identifies 15 habitat elements that may affect 1 or more critical biological activities or processes among the 3 LLFR life stages. Some of these habitat elements differ in their details among life stages (e.g., different species may prey on different life stages of LLFR). However, using the same labels for the same *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 LLFR conceptual ecological model includes habitat elements identified in species accounts and scientific studies demonstrating or positing a direct effect on one or more critical biological activities or processes for one or more LLFR life stages or for similar or related species in similar habitats. Table 3 lists the 15 habitat elements and the critical biological activities or processes that they may *directly* affect across all LLFR life stages. Habitat elements may also directly affect each other.

Except where noted, the sources of the information in this chapter are the AZGFD Heritage Data Management System Animal Abstract for LLFR (AZGFD 2006), the most recent LCR MSCP species account (LCR MSCP 2016), Sartorius and Rosen (2000), and the online accounts by Rorabaugh (2018b) and Sredl (2018). These publications summarize all earlier studies. Where appropriate and accessible, those earlier studies are directly cited. The identification also integrates information from the expert knowledge of LCR MSCP biologists and from more recent studies, including investigations by Rosen et al. (2013) and others (Parker 2006; Swann and Wallace 2010; Wallace et al. 2010) in southeastern Arizona and by the AZGFD in the LCR, Bill Williams, Agua Fria, and Verde River valleys (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b). In addition, where appropriate, the discussions of individual critical biological activities and processes draw upon literature concerning leopard frogs of the Southwestern United States or larger classes of frogs in general. The results are hypotheses that make the best use of the available information.

The following paragraphs discuss the 15 habitat elements in alphabetical order. As with all such tabulations of habitat associations, inferences that particular habitat characteristics may be critical to a species or life stage require evidence and CEMs for why each association matters to species viability (Rosenfeld 2003; Rosenfeld and Hatfield 2006).

Table 3.—LLFR habitat elements and the critical biological activities and processes that are proposed to directly affect them among the three life stages
(Xs indicate which habitat elements may affect each critical biological activity or process.)

Affected critical biological activity or process ➔ / **Causal habitat element 🡻**	**Chemical stress**	**Competition**	**Disease**	**Foraging**	**Hybridization**	**Hydration stress**	**Mating and ovipositing**	**Mechanical stress**	**Occupancy and inter-site movement**	**Predation**	**Resting/hiding**	**Thermal stress**
Airborne contaminants	X											
Birds and mammals		X								X		
Drainage network connectivity									X			
Fire regime												X
Fish and herpetofauna		X		X	X					X		
Herbaceous vegetation				X			X		X		X	
Hydrologic regime						X	X	X	X		X	
Infectious agents			X									
Macroinvertebrates		X		X						X		
Monitoring, capture, handling						X		X			X	
Periphyton and particulate organic matter (POM)				X								
Substrate								X			X	
Water chemistry	X											
Water temperature							X					X
Woody vegetation							X		X		X	

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a one-to-three-word short name; however, each short name in fact refers to a longer, complete name. For example, “fire regime”

is the short name for "The frequency, timing, spatial extent, and severity of fire at locations with or potentially suitable for LLFR habitat and their immediate surroundings, as affected both by natural fuel and ignition dynamics and by management actions including prescribed burns." The following paragraphs provide both the short and full names for each habitat element and a detailed definition, addressing the elements in alphabetical order.

AIRBORNE CONTAMINANTS

Full name: **The concentrations of chemical contaminants carried by the air into locations with or potentially suitable for LLFR habitat within the LCR ecosystem that could harm LLFR or species with which LLFR interact**. This habitat element addresses chemicals that may drift in the air to reach LLFR from land-use activities upwind. In principal, the element includes herbicides, pesticides, fertilizers, and industrial wastes. The literature reviewed and experts consulted to prepare this CEM do not identify any specific airborne chemical contaminants of potential concern for LLFR habitat sites along the LCR or Bill Williams River valleys. However, airborne pesticide drift from agricultural spraying is a frequently noted suspect in amphibian declines in Arizona, the Western United States, and worldwide (Blaustein et al. 2003; Brühl et al. 2013; Davidson et al. 2002; Hayes and Jennings 1986; Mann et al. 2009; Smalling et al. 2015; Sredl et al. 1997b).

Agricultural fields occur in close proximity to potential LLFR habitat sites identified by the AZGFD along the main stem LCR valley (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014). Herbicides and pesticides are widely used on alfalfa and cotton, which are both grown extensively in the LCR valley, with aerial application common. The possibility therefore exists for airborne contaminants to disperse into potential LLFR habitat sites. However, the LCR MSCP does not have access to data on chemical use on the agricultural fields in the LCR valley (J. Hill and C. Ronning 2018, joint personal communication).

Atmospheric deposition of mercury may also pose a risk to LLFR along the LCR and Bill Williams River valleys. Atmospheric mercury causes harm not through direct contact during its deposition but through its movement into the food web following deposition and conversion to a biologically active form in the right aquatic environment (Bank et al. 2007; Unrine et al. 2004). As discussed below (see below, this chapter, "Water Chemistry"), mercury presumed to be from atmospheric deposition has been found in fish tissue along the LCR and in Alamo Lake on the Bill Williams River. Other members of the genus *Lithobates* (*Rana*) may bioaccumulate mercury even as larvae (Bank et al. 2007; Unrine et al. 2004).

BIRDS AND MAMMALS

***Full name*: The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity levels of the assemblages of birds and mammals that may visit or occupy LLFR habitat within the LCR ecosystem**. This element refers to the range of bird and mammal species known or suspected to interact with LLFR or its habitat along the LCR valley and its tributary watersheds. This range includes species known, suspected, or potentially able to prey on LLFR eggs, larvae, or adults.

As noted in chapter 3, "Predation," the general literature on frogs recognizes wading birds, such as bitterns and herons, and small mammals, as potential predators (Duellman and Trueb 1986; Wells 2007). However, as also noted in chapter 3, "Predation," there are few direct observations of predation on LLFR in any life stage.

Two bird species included in the mandate for the LCR MSCP prey on frog larvae and adults generally and, therefore, likely prey on LLFR larvae and adults in the greater LCR ecosystem. The Yuma clapper rail (*Rallus longirostris yumanensis*) preys on tadpole and adult frogs in general, including American bullfrog tadpoles (LCR MSCP 2016). The least bittern also preys on frogs, particularly members of the genus *Lithobates* (*Rana*) (LCR MSCP 2016).

The LCR MSCP (2016) species account for LLFR specifically mentions great blue herons as predators of LLFR larvae, although it does not cite a source for this information. Additionally, investigators in recent years have expanded the list of bird species known or suspected to prey on native fishes along the LCR, and several of these are known in other settings to consume frog larvae and adults as well (Best 2015; Best et al. 2017; Humphrey et al. 2014, 2015, 2016; Kesner et al. 2008; Lantow 2017; LCR MSCP 2017; McCall et al. 2017; Mueller 2006, 2017). The resulting list of other bird species in the LCR ecosystem that also may consume LLFR larvae and adults includes the belted kingfisher *(Megaceryle alcyon*), double-crested cormorant (*Phalacrocorax auratus*), great egret (*Ardea alba*), and possibly other egret species such as green heron (*Butorides virescens*), and the black-crowned night heron (*Nycticorax nycticorax*).

The 1997 "Riparian Herp Survey Form" for the AZGFD (Sredl et al. 1997b) also suggests that field investigators look for signs of possible predation on Arizona leopard frogs by three other bird species: American bitterns *(Botaurus lentiginosus*), zone-tailed hawks (*Buteo albonotatus*), and black hawks (*Buteogallus anthracinus*). However, this form was designed as a general-purpose tool during field surveys for reptiles and amphibians and not specifically as a tool for investigating leopard frogs (Sredl et al. 1997b).

General species accounts for the LLFR identify several native mammals as potential predators of LLFR eggs, larvae, or adults across the historic range of LLFR, as also noted above (see chapter 3, "Predation"). The strongest candidates for a list of mammal species that may prey on LLFR in the greater LCR ecosystem are three species identified by Mueller (2006) that hunt for fishes along the shores and shallows of streams and wetlands along the LCR valley: coyotes (*Canis latrans*), raccoons (*Procyon lotor*), and ringtail cats (*Bassariscus astutus*).

The 1997 "Riparian Herp Survey Form" for the AZGFD (Sredl et al. 1997b) also suggests that field investigators look for signs of possible predation by eight other native and non-native mammals: bobcats (*Felis rufus*), striped skunks (*Mephitis mephitis*), coatis (*Nasua nasua*), mountain lions (*Puma concolor*), the non-native common or Norwegian rat (*Rattus norvegicus*), western spotted skunks (*Spilogale gracilis*), badgers (*Taxidea taxus*), and the gray fox (*Urocyon cinereoargenteus*). The form also mentions the American black bear (*Ursus americanus*) as a possible predator of LLFR, but this species does not occur along the LCR valley. Again, however, this form was designed as a general-purpose tool during field surveys for reptiles and amphibians and not specifically as a tool for investigating leopard frogs (Sredl et al. 1997b).

The intensity, timing, and geographic distribution of foraging by birds and mammals presumably depends on more than simply the presence and abundance of the potential predators. Other habitat elements that may also affect the activity levels of potential bird and mammal predators include the season and time of day, air temperature and other weather conditions, flow and wave activity, turbidity, or the availability of perch or cover habitat for the predators. Further, LLFR vulnerability to bird or mammal predation may also depend on some of these same factors and the availability of vegetative cover and other hiding places for the frogs (see chapter 3, "Resting/Hiding"). LLFR adults may also be particularly vulnerable to bird or mammal predation during inter-site movement across open ground between water bodies, but LLFR evolved in a predator-rich environment, as indicated by the large number of its potential native bird and mammal predators. As discussed above (see chapter 3, "Predation" and "Resting/Hiding"), LLFR exhibit behaviors that appear to help them avoid predation or maintain their abundance despite pressure at least from native predators.

At least two other native mammals, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*), may affect LLFR in the LCR ecosystem not through predation but by shaping habitat. These two species once were common in the LCR ecosystem, where they helped shape mesohabitat conditions by introducing woody debris and creating marshes and pools along backwater channels (Grinnell 1914; Kniffen 1932; Minckley and Rinne 1985; Ohmart et al. 1988; Stevens et al. 1997). Both species are still present along the LCR and Bill Williams River valleys and are increasingly shaping habitat again today (Boutwell 2002; Hautzinger 2010; Kesner et al. 2008; Montony 2010; Mueller 2006; Mueller et al. 2005; Shafroth and Beauchamp 2006).

The possible effects of beaver and muskrat activity on LLFR have not been systematically investigated but may be both beneficial and detrimental. AZGFD (2006) and Sredl (2018) specifically identify ponds behind beaver dams as LLFR habitat. Cotten and Grandmaison (2013) state that high beaver activity along a section of the Bill Williams River helped "… maintain fluctuating water levels and pathways, which has limited colonization of saltcedar (*Tamarix* spp.) and promoted growth of native wetland vegetation." On the other hand, Miller and Leavitt (2015) and O'Donnell and Leavitt (2017a, 2017b) found a high density of saltcedar around "… extensive beaver impoundments" along the same section of the Bill Williams River Valley and note that the combination of these conditions greatly impaired the feasibility of surveying for LLFR. Rosen et al. (2013) similarly caution that the pools created by beavers in wetland areas can favor the growth of non-native plants. Both beavers and muskrats also eat aquatic macrophytes and, thereby, may both shape macrophyte availability and generate POM at the same time (Henker 2009), potentially affecting breeding and cover habitat for LLFR adults and food availability for LLFR larvae.

Finally, the possible effects of grazing by native mule deer (*Odocoileus hemionus*) and non-native cattle (*Bovidae*) and burros (*Equus asinus*) on LLFR also are not clear. Grazing by cattle and burros across the arid Southwest (Sredl et al. 1997b) can degrade riparian habitat (USFWS 2002 – Appendix G), by thinning the understory or preventing the establishment of cottonwood (*Populus* spp.) and willow (*Salix* spp.) 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.

On the other hand, mere trampling of habitat by cattle or burros does not appear to bother LLFR, as evidenced by their frequently reported use of earthen cattle tanks as habitat and their use of puddles in cattle hoof prints for resting/hiding (see chapter 3). The USFWS (2016) also has noted specifically for the closely related relict leopard frog that

> *[b]urro and cattle grazing have both degraded and improved aquatic habitat at some sites. Controlled, low-level grazing typically provides disturbance that benefits frog habitat by removing excess vegetation. If grazing increases to heavy use, habitat conditions may become degraded. Similarly, burro and cattle grazing are not having a population-level effect to the relict leopard frog now or into the future.*

As noted in chapter 3 (see "Resting/Hiding"), it does not appear to be unusual for anurans in general to use cattle hoof prints as aquatic refuge and stepping-stone habitat (Pelinson et al. 2016). More generally, Howell et al. (2019), reporting on the results of one empirical study of the impacts of cattle on amphibian communities and a quantitative literature review of similar studies on five continents, found that

> *... amphibian species that historically occurred in closed-canopy habitats are generally negatively affected by livestock presence. In contrast, open-canopy amphibians are likely to experience positive effects from the presence of livestock, and these positive effects are most likely to occur in locations with cooler climates and/or greater precipitation seasonality. Collectively, our empirical work and literature review demonstrate that under the correct conditions well-managed rangelands are able to support diverse assemblages of amphibians.*

However, no studies have explicitly examined the impacts of cattle or burro activity on LLFR site use or behaviors.

Non-native, feral pigs (*Sus scrofa*) also can disturb riparian habitat; however, although they occur and are regarded as a nuisance in Havasu National Wildlife Refuge (Neskey 2018; U.S. Department of the Interior 2016), the literature does not mention them affecting habitat conditions at LCR MSCP sites.

DRAINAGE NETWORK CONNECTIVITY

Full name: **The capacity of a surface water drainage network to support or inhibit both upstream and downstream movement of aquatic organisms, as determined by the spatial distribution of natural and artificial barriers, including falls and dry reaches that may prevent or inhibit such movement**. Drainage networks may include natural water courses, artificial water courses such as diversion and drainage channels, and artificial water bodies such as impoundments. Drainage network connectivity affects the taxonomic and genetic composition of the fish and frog assemblages in different reaches of a drainage network by affecting the ability of these fauna to move within the network, including escaping reaches of the network that have become isolated by interruptions in drainage network connectivity, returning to reaches previously isolated by such interruptions, or colonizing new habitat (e.g., cattle tanks) created by human activities (Benda et al. 2004; Fullerton et al. 2010; Levick et al. 2008; Meyer et al. 2007; Perkin and Gido 2012; Pilger et al. 2015; Pringle 2003; Turner and List 2007). For a given water-dependent species or group of species, the severity of fragmentation (loss of connectivity) in a drainage network depends on the number and spatial extent of barriers, their relative placement within the network, and their permeability (ability to allow some passage of the subject fauna) (Fullerton et al. 2010).

As discussed in chapter 3 (see "Occupancy and Inter-Site Movement"), genetic data collected by Goldberg et al. (2004 *in* LCR MSCP 2016) in the Rincon Mountains in Saguaro National Park indicate that LLFR inter-site movement occurs only or overwhelmingly along drainage lines. Instances of LLFR inter-site movement reported by Sredl et al. (1997a) and Howland et al. (1997) also exclusively involve movement within single drainages. As noted in chapter 3 (see "Occupancy and Inter-Site Movement"), Witte et al. (2008) used the AZGFD database of native ranid frog historic and current occurrences in Arizona to assess factors that might be associated with local disappearances of native ranid frogs, including the proximity of occupied versus depopulated sites to each other. They found that the odds of ranid frogs disappearing from an individual site were significantly greater if they had also disappeared from another site within 6 km, eliminating a nearby source for recolonization. Conversely, Witte et al. (2008) found that the odds of ranid frogs disappearing from an individual site were significantly less if they had not also disappeared from another site within 4 km; however, the study measured site proximity in terms of air distance rather than distance within drainage networks. Consequently, the study results do not provide clear information on the role of drainage network connectivity or fragmentation in LLFR movement and population declines.

On the other hand, as also discussed above (see chapter 3, "Occupancy and Inter-Site Movement"), Zylstra et al. (2015) used mark-resight data from 2013 in the Rincon Mountains in Saguaro National Park to assess the frequency and distances of adult LLFR movement within versus between pool complexes along drainage courses. Each pool complex consisted of closely adjacent pools that functioned as integrated habitat because of their close proximity (< 120 m separation when surface water was not present outside of the surveyed pools). Their results indicate that adult LLFR were significantly less likely to move between pool complexes, versus moving only within their natal pool complex. Only 7 (5%) of 129 movements occurred between complexes, including only 1 that occurred when there was no surface water between the 2 pool complexes (Zylstra et al. 2015). The study of inter-site movement among Chiricahua leopard frogs by Hinderer et al. (2017) similarly found that such movements were more likely when water was present between pools along stream courses (although not during high flow events).

Most remaining populations of LLFR in Arizona are small and isolated (Sartorius and Rosen 2000; see discussion of genetic fragmentation in chapter 2, "LLFR Life Stage 3 – Adults). The literature consistently identifies losses of drainage network connectivity, both within and between watersheds across the historic range of LLFR, as a leading cause of the collapsing geographic distribution of LLFR and/or similar collapses among other ranid frogs of the Western United States (AZGFD 2006; Hayes and Jennings 1986; LCR MSCP 2016; Sredl 2018; Sredl et al. 1997b). The leading causes of drainage network fragmentation identified in this literature include direct habitat loss as a result of stream diversions and groundwater withdrawals that eliminate surface water flow,

habitat destruction by severe sedimentation, and occupation of LLFR habitat by highly effective predators and/or competitors such as the American bullfrog. On the other hand, as discussed below (see below, this chapter, "Hydrologic Regime"), LLFR evolved in adaptation to at least some natural hydrologic fragmentation (Sartorius and Rosen 2000; see chapter 1, "Lowland Leopard Frog Reproductive Ecology") to which at least some non-native predators may not be well adapted. As noted by Cotten and Grandmaison (2013), "The canyons of southeastern Arizona are under constant threat of drought and are frequently cut off from perennial water sources. Consequently, these arroyos and canyon pools may remain relatively free of predatory fishes and bullfrogs, which are less adapted to periods of drought and flood." Discussing specifically the reaches of the Bill Williams River below Alamo Dam occupied by LLFR, Cotten and Leavitt (2014) note "Surface water becomes more ephemeral and often percolates into the sand near the Bill Williams River National Wildlife Refuge eastern boundary and onto Planet Ranch. This section has fewer predators and an abundance of small ephemeral pools ideal for amphibian breeding."

Similarly, as noted in chapter 1, the literature recognizes the genetic isolation of local populations as a common problem for LLFR throughout their range as a result of impaired drainage network connectivity that prevents adult movement between populations (Rosen et al. 2013). For example, the study by Goldberg et al. (2004 *in* LCR MSCP 2016) found genetic evidence of recent population bottlenecks that had persisted through an estimated 17 generations in 4 of 7 populations tested. The study authors suggest that these bottlenecks resulted from the drying up of much of the drainage network in the study area.

FIRE REGIME

Full name: **The frequency, timing, spatial extent, and severity of fire at locations with or potentially suitable for LLFR habitat within the LCR ecosystem and their immediate surroundings**. Wildfire is a natural type of disturbance in the riparian plant communities of the LCR and similar ecosystems in the Southwestern United States, and wildfires today also occur through human causes (Conway et al. 2010; LCR MSCP 2013, 2018a; Meyer 2005; Stromberg et al. 2009). The LCR MSCP uses prescribed fire as a tool for habitat management (LCR MSCP 2018a). Wildfires also can spread from uplands into marshes along the LCR (Anderson 2012), where residual and/or seasonally dry vegetation may provide highly combustible fuel (Conway et al. 2010).

A fire burning across a site occupied by LLFR or containing potential LLFR habitat could directly affect LLFR and its habitat in two ways. First, such a fire presumably would raise both air and water temperatures, thereby killing eggs and any larvae or adults unable to find refuge underground or in deeper water. However, the literature on LLFR contains no records of this type of occurrence. On the other hand, the broader literature on the effects of fire through riparian

corridors recognizes the potential for such fatal effects on aquatic biota in general (Brown et al. 2001; Brunelle and Minckley 2002; Dunham et al. 2003; Gresswell 1999; Luce et al. 2012; Whitney et al. 2015).

Second, fire burning across a site occupied by LLFR or containing potential LLFR habitat could affect riparian and marsh vegetation composition, structure, and succession (Brown et al. 2001; Brunelle and Minckley 2002; Gresswell 1999; Luce et al. 2012; Nagler et al. 2011; Stromberg et al. 2009; Whitney et al. 2015). Stromberg et al. (2009), for example, looked at the effects of reintroducing fire into the riparian corridor of the San Pedro River in Arizona after a period of fire suppression. The authors found that fire significantly reduced woody vegetation, and reset succession in the woody vegetation assemblage, and also resulted in "… a short-term pulse of herbaceous plant diversity, driven by annual species, and [a] persistent increase in herbaceous cover." The authors also found evidence that "… the increase in herbaceous cover was mediated in part by the reduction in tree canopy cover." They conclude that allowing or restoring fire in the riparian corridor will "… shift [the] structure of the Upper San Pedro floodplain vegetation closer toward conditions present during past centuries when fire was frequent in the upland desert grasslands and embedded riparian corridor." The abundance of fuel from dried herbaceous vegetation and from both living and dead woody vegetation conversely affects the spatial extent and severity of fire in riparian settings. Such changes in habitat conditions in turn could affect LLFR abundance at the affected sites (see below, this chapter, "Herbaceous Vegetation," and "Woody Vegetation").

Upland wildfire in watersheds with LLFR habitat can also indirectly affect LLFR. Parker (2006) describes how upland fires in some watersheds in the Rincon Mountains in Saguaro National Park resulted in increased soil erosion from these watersheds, resulting in the filling of former pools with sediment, thereby causing local extirpations of LLFR.

FISH AND HERPETOFAUNA

Full name: **The taxonomic, functional, and size composition; spatial and temporal distributions; abundance; and activity level of fishes, reptiles, and other amphibians that may interact with LLFR or its habitat along the LCR valley**. Interactions may include predation on LLFR eggs, larvae and juveniles, or adults; competition for food or habitat with LLFR larvae-juveniles or adults; and habitat alteration. Most of the fishes of interest are non-native, while most of the herpetofauna are native. Activity levels may vary in response to other habitat conditions, such as water availability and depth; flow velocities, temperature, or chemistry; or the quality of wetland and riparian vegetation.

As noted in chapter 3, "Predation," the general literature on frogs recognizes other amphibians such as stream salamanders and bullfrogs, reptiles such as snakes and turtles, and a wide range of fishes as potential predators (Duellman and Trueb 1986; Wells 2007). However, as also noted above (see chapter 3, "Predation") there are few direct observations of predation on LLFR in any life stage.

As noted earlier, Cotten and Leavitt (2014) assessed the extent to which the presence of several classes of predators predicts LLFR habitat use along the LCR (Reaches 3–7) and along the Bill Williams River below Alamo Dam, and found that the presence of sunfish and largemouth bass strongly suppress LLFR numbers in this study area. Cotten and Grandmaison (2013) and Cotten and Leavitt (2014) identify the relatively low abundances of non-native fishes along the Bill Williams River below Alamo Dam as one likely reason for the persistence of LLFR in these waters (see above, this chapter, "Drainage Network Connectivity").

Table 4 lists all fishes reported in the present-day LCR ecosystem downstream from Hoover Dam (Gloss and Coggins 2005; ; Marsh and Pacey 2005; Minckley 1991; Minckley et al. 2003; Mueller and Marsh 2002 Ohmart et al. 1988; Pool et al. 2010; U.S. Geological Survey [USGS] Nonindigenous Aquatic Species Program 2018). Table 4 does not include species introduced into the LCR prior to 1975 (as listed by Miller 1952 and Mueller and Marsh 2002) that do not appear in more recent records and, therefore, likely no longer occur in the LCR. Table 4 also includes species that occur in the Bill Williams River but may not occur in the main stem LCR valley (Shafroth and Beauchamp 2006).

Table 4 indicates whether each fish species is native (N) or introduced (I); whether any life stages of the species is known to prey on LLFR eggs, larvae, or adults (X), or potentially could, do so (?); and whether any life stage of the species is known to compete with LLFR larvae or adults for food or habitat (X) or potentially could do so (?). Inferences about the potential of a species to prey on or compete with LLFR rest on information in the databases of Froese and Pauly (2018), NatureServe Explorer (NatureServe 2018), the USGS Nonindigenous Aquatic Species Program (2018), and the LCR MSCP conceptual ecological models for the razorback sucker (*Xyrauchen texanus*) (Braun 2018a), flannelmouth sucker (*Catostomus latipinnis*) (Braun 2018b), and bonytail (*Gila elegans*) (Braun 2018c). The criteria for these determinations are as follows:

- Table 4 identifies a fish species as a known predator of LLFR in one or more life stages based on the evidence presented by Rosen et al. (2013) concerning fish predation on LLFR larvae.

- Table 4 identifies a fish species as a potential predator of LLFR eggs or larvae and juveniles if the aforementioned sources indicate that one or more life stages of the species: (a) may prey on amphibian eggs or larvae, on fish eggs, or on small fishes and (b) may do so in shallow waters, including wetlands, smaller streams, or shorelines or backwaters of larger streams and rivers.

Table 4.—Fish species in the LCR ecosystem that may prey on or compete with LLFR

Species	Origin	$Prey_{EL}$	$Prey_{A}$	$Comp_{E/L}$	$Comp_{A}$
Black bullhead (*Ameiurus melas*)	I	X	?	?	?
Black crappie (*Pomoxis nigromaculatus*)	I	?			?
Bluegill (*Lepomis macrochirus*)	I	X	?		?
Bonytail (*Gila elegans*)	N	?		?	?
Brown trout (*Salmo trutta*)	I	?	?		?
Channel catfish (*Ictalurus punctatus*)	I	X	?		
Common carp (*Cyprinus carpio*)	I	?		?	?
Cutthroat trout (*Oncorhynchus clarkia*)	I	?			?
Desert pupfish (*Cyprinodon macularius*)	N			?	
Fathead minnow (*Pimephales promelas*)	I	?		?	?
Flannelmouth sucker (*Catostomus latipinnis*)	N			?	
Flathead catfish (*Pylodictis olivaris*)	I	X			?
Gila chub (*Gila intermedia*)	N	X	?	?	
Gizzard shad (*Dorosoma cepedianum*)	I			?	
Golden shiner (*Notemigonus crysoleucas*)	I			?	
Goldfish (*Carassius auratus*)	I	?		?	?
Green sunfish (*Lepomis cyanellus*)	I	X	?		?
Humpback chub (*Gila cypha*)	N	?		?	?
Largemouth bass (*Micropterus salmoides*)	I	X	?		?
Longfin dace (*Agosia chrysogaster*)	N			?	
Mouthbrooder (*Tilapia mossambica*)	I	?	?	?	?
Rainbow trout (*Oncorhynchus mykiss*)	I	?	?		?
Razorback sucker (*Xyrauchen texanus*)	N			?	
Red shiner (*Cyprinella lutrensis*)	I				?
Redbelly tilapia (*Tilapia zillii*)	I	X		?	?
Redear sunfish (*Lepomis microlophus*)	I	?			
Roundtail chub (*Gila robusta*)	N	?		?	?
Sailfin molly (*Poecilia latipinna*)	I			?	
Smallmouth bass (*Micropterus dolomieu*)	I	?	?		?
Sonora sucker (*Catostomus insignis*)	N			?	?
Sonoran topminnow (*Poeciliopsis occidentalis*)	N			?	
Speckled dace (*Rhinichthys osculus*)	N			?	
Striped bass (*Morone saxatilis*)	I	?	?		?
Threadfin shad (*Dorosoma petenense*)	I	?		?	
Walleye (*Sander vitreus*)	I	?	?		?
Warmouth sunfish (*Lepomis gulosus*)	I	?	?		?
Western mosquitofish (*Gambusia affinis*)	I	?		?	?
White bass (*Morone chrysops*)	I	?	?		?
White crappie (*Pomoxis annularis*)	I	?			?
Woundfin (*Plagopterus argentissimus*)	N			?	?
Yellow bullhead (*Ameiurus natalis*)	I	?	?	?	?
Yellow perch (*Perca flavescens*)	I	?			?

Origin: "I" = introduced; "N" = native.
$Prey_{EL}$: Does or could species prey on LLFR eggs or larvae? (see key below)
$Prey_{A}$: Does or could species prey on LLFR adults? (see key below)
$Comp_{EL}$: Does or could species compete with LLFR eggs or larvae for food or habitat? (see key below)
$Comp_{A}$: Does or could species compete with LLFR adults for food or habitat? (see key below)

Key to predation and competition columns: "X" = reported in literature; "?" = suggested by species data in Froese and Pauly (2018), NatureServe Explorer (NatureServe 2018), the USGS Nonindigenous Aquatic Species Program database (USGS 2018), or LCR MSCP conceptual ecological models for the bonytail, flannelmouth sucker, or razorback sucker.

- Table 4 identifies a fish species as a potential predator of LLFR adults if the aforementioned sources indicate that one or more life stages of the species: (a) may prey on amphibian adults or on fishes of a similar or larger size compared to LLFR adults and (b) may do so in shallow waters, including wetlands, smaller streams, or shorelines or backwaters of larger streams and rivers.

- Table 4 identifies a fish species as a potential competitor for food or habitat with LLFR larvae if the aforementioned sources indicate that one or more life stages of the species: (a) have herbivorous diets similar to that of LLFR larvae; (b) may feed in wetlands, smaller streams, or shorelines or backwaters of larger streams and rivers; and (c) prefer habitat conditions similar to those preferred by LLFR larvae, such as shallow, clear, cool to warm, non-stagnant waters with moderate densities of aquatic vegetation and canopy cover.

- Table 4 identifies a fish species as a potential competitor for food or habitat with LLFR adults if the aforementioned sources indicate that one or more life stages of the species: (a) have carnivorous diets similar to that of LLFR adults; (b) may feed in wetlands, smaller streams, or shorelines or backwaters of larger streams and rivers; and (c) prefer habitat conditions similar to those preferred by LLFR adults, such as shallow, clear, cool to warm, non-stagnant waters with moderate densities of aquatic vegetation and canopy cover. Fishes that may prey on aquatic insect larvae were considered potential competitors because such consumption could reduce the abundance of the adult life stages of these insect species on which LLFR adults otherwise would prey.

Other studies provide additional information in support of the inferences in table 4. Rosen et al. (2013) specifically note that LLFR readily co-exist with Gila topminnow (*Poeciliopsis occidentalis*) and desert pupfish, which also readily co-exist with each other. These authors further note the following:

> [Gila topminnow and desert pupfish] *... are lowland species ... that do not thrive under the rigorous flood regime of canyon-bound streams that protects some native Southwestern fishes from being displaced by non-native species…. Topminnow and pupfish, alone or in combination, appear to have little effect on reproductive success of lowland leopard frogs.*

One fish species listed in table 4 also may affect habitat quality for LLFR. The common carp (*Cyprinus carpio*) disturbs benthic sediments during feeding and spawning (Cucherousset and Olden 2011; Rogers et al. 2008), which may also cause localized but temporary increases in turbidity. LLFR prefer habitat settings with stable sediment and clear water (see below, this chapter, "Hydrologic Regime" and "Substrate"). As discussed in chapter 1 (in the detailed discussions of the three life stages), several reptiles that occur in the greater LCR ecosystem

are known or strongly suspected to prey on LLFR eggs, larvae-juveniles, and/or adults. These include the black-necked garter snake, the distribution of which extends into the eastern headwaters of the Bill Williams River watershed (AZGFD 2019), and the northern Mexican gartersnake.[5] As also discussed in chapter 1 (in the detailed discussions of the three life stages), several amphibians that occur in the greater LCR ecosystem also are known or strongly suspected to prey on LLFR eggs, larvae-juveniles, and/or adults, and particularly include the non-native Rio Grande leopard frog and American bullfrog. Both species may also compete with LLFR eggs, larvae-juveniles, and/or adults for food and habitat (see chapter 3, "Competition"). Cotten and Grandmaison (2013) and Cotten and Leavitt (2014) identify the relatively low abundances of non-native frogs along the Bill Williams River below Alamo Dam as another likely reason for the persistence of LLFR in these waters (see above, this chapter, "Drainage Network Connectivity"). Two of the basic species accounts for LLFR (LCR MSCP 2016; Sredl 2018) also identify adult LLFR as suspected predators (cannibals) of LLFR larvae.

Beyond this limited list of likely or possible herpetofauna specifically identified in the literature that may affect LLFR in the greater ecosystem, it is useful to look at the spectrum of herpetofauna that also occur in this ecosystem for other species that may interact with LLFR. Ohmart et al. (1988), Cotten and Grandmaison (2013; also see Cotten and Leavitt 2014), O'Donnell and Leavitt (2017b), and the USFWS (2018) identify the herpetofauna known to occur along the LCR valley in general, along the Bill Williams River, and at the Cibola National Wildlife Refuge, respectively. Additional information regarding herpetofauna at LCR MSCP conservation areas is not available.

Ohmart et al. (1988) tabulate all records of herpetofauna in the LCR ecosystem up to 1982, identifying 55 species. Cotten and Grandmaison (2013), O'Donnell and Leavitt (2017b) and USFWS (2018) provide lists based only on contemporary records, identifying 10, 21, and 34 species, respectively. Cotten and Grandmaison (2013) specifically identify all amphibians located during AZGFD surveys of potential habitat for LLFR and the Colorado River toad along the main stem LCR and Bill Williams River valleys. O'Donnell and Leavitt (2017b) specifically identify all other reptiles and amphibians observed during AZGFD monitoring along the Bill Williams River also otherwise focused on LLFR and the Colorado River Frog. Hill (J. Hill 2019, personal communication) recently confirmed

[5] The LCR MSCP species account for LLFR (2016) also specifically mentions mud turtles as a possible predator of LLFR in the LCR ecosystem; however, neither of the two mud turtle species that occur in Arizona—the Arizona mud turtle (*Kinosternon arizonense*) and Sonora mud turtle (*Kinosternon sonoriense*)—occurs in or near the greater LCR ecosystem (https://www.azgfd.com/wildlife/nongamemanagement/turtle/mud-turtles/)

the presence of the Sonoran lyre snake (*Trimorphodon lambda*) in the lower Bill Williams River valley based on an individual photographed in the Planet Ranch section of the valley in 2014.[6]

The herpetofauna species lists in the aforementioned sources broadly overlap (after standardizing nomenclature), differing mainly in the inclusion of larger numbers of species in Ohmart et al. (1988) and USFWS (2018) associated with xeric habitat. A merged list includes 576 species, including the two garter snakes, a lyre snake, and two non-native frogs (Rio Grande leopard frog and American bullfrog). A review of basic ecological information on these 56 species indicates that 18 may occur in, and potentially could prey on, one or more life stages of LLFR along the LCR and Bill Williams River valleys. Table 5 lists these 18 species, including three non-natives, alphabetically by common name, and explains why each is or should be considered a likely or possible predator of LLFR. Scientific nomenclature follows NatureServe (2018). Several of the species in table 5, particularly the majority of the snakes, forage in both upland and riparian habitat.

Without direct observations, it is difficult to identify those herpetofauna listed by O'Donnell and Leavitt (2017b), Ohmart et al. (1988), and the USFWS (2018) that possibly could compete with LLFR for food or habitat along the LCR and Bill Williams River valleys. The larvae of all amphibians are aquatic, and all are herbivorous during at least some portion of this life stage. The aforementioned three sources identify nine amphibians other than LLFR that occur in these valleys, including the Great Plains toad (*Anaxyrus cognatu*s), Arizona toad (*Anaxyrus microscaphus*), red-spotted toad (*Anaxyrus punctatus*), Woodhouse's toad (*Anaxyrus woodhousii*), Canyon treefrog (*Dryophytes arenicolor*), Colorado River toad, Rio Grande leopard frog, American bullfrog, and Couch's spadefoot toad (*Scaphiopus couchii*). However, except for the Rio Grande leopard frog and American bullfrog, the amphibians that occur along the LCR and Bill Williams River valleys are native to the region and use aquatic and wetland habitat, a spatially very limited and highly variable resource in the region. LLFR likely co-evolved with these other native amphibians in ways that reduce competition for such scarce resources, possibly including some resource partitioning. The Colorado River toad, for example, breeds in seasonal, ephemeral pools, while LLFR almost exclusively inhabit permanent or nearly permanent surface water bodies and do not rely on ephemeral pools for breeding (O'Donnell and Leavitt 2017a, 2017b; Sartorius and Rosen 2000; also see below, this chapter).

[6] Ohmart et al. (1988) also list the American alligator (*Alligator mississippiensis*), eastern tiger salamander (*Ambystoma tigrinum*), Arizona treefrog (*Hyla eximia*), and Texas lyre snake (*Trimorphodon vilkinsonii*), but no sources recognize any of these species as currently occurring in the greater LCR ecosystem. On the other hand, the reference to the Texas lyre snake may refer to the Sonoran lyre snake noted in table 5.

Table 5.—Reptile and amphibian species in the LCR ecosystem that may prey on LLFR

Species	Reasoning
American bullfrog (*Lithobates catesbeianus*)	Introduced. Likely predator of all life stages of LLFR. Brennan (2008), LCR MSCP (2016), NatureServe (2018), Rosen et al. (2013), Sredl (2018), and USFWS (2017) all note that this generalized carnivore is known to eat other amphibians, its larvae are carnivorous and known to eat the larvae of other amphibians, and its presence almost always results in greatly reduced LLFR abundance.
Black-necked gartersnake (*Thamnophis cyrtopsis*)	A known predator of LLFR across the eastern portions of the LLFR range (Jones 1990 *in* Sredl 2018), the current distribution of which includes eastern headwaters of the Bill Williams River watershed (AZGFD 2019).
California kingsnake (*Lampropeltis californiae*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (CaliforniaHerps 2019).
Checkered gartersnake (*Thamnophis marcianus*)	Likely predator of all life stages of LLFR—a generalized carnivore known to eat frogs and tadpoles (Brennan 2008; NatureServe 2018). The related black-necked gartersnake is a known predator of LLFR across the eastern portions of the LLFR range (Jones 1990 *in* Sredl 2018).
Coachwhip (*Coluber flagellum*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008).
Colorado River toad (*Incilius alvarius*)	Possible predator of LLFR adults—a generalized carnivore known to eat other amphibians (Brennan 2008; NatureServe 2018).
Common kingsnake (*Lampropeltis getula*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008; NatureServe 2018).
Couch's spadefoot toad (*Scaphiopus couchii*)	Possible predator of LLFR larvae-juveniles: Brennan (2008) reports that its tadpoles are carnivorous and known to cannibalize, raising the possibility that it could prey on larvae of other amphibians as well.
Desert glossy snake (*Arizona elegans*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008; NatureServe 2018).
Desert nightsnake (*Hypsiglena chlorophaea*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008; NatureServe 2018).
Gopher snake (*Pituophis catenifer*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008).
Mohave rattlesnake (*Crotalus scutulatus*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008).
Northern Mexican gartersnake (*Thamnophis eques megalops*)	Likely predator of all life stages of LLFR (see chapter 1)—a generalized carnivore known to eat frogs and tadpoles (Brennan 2008; NatureServe 2018).
Pond slider (*Trachemys scripta*)	Introduced. Possible predator of LLFR larvae-juveniles—a generalized carnivore, younger individuals of which are known to eat amphibian larvae (Brennan 2008; NatureServe 2018).
Red-spotted toad (*Anaxyrus punctatus*)	Possible predator of LLFR larvae-juveniles: Brennan (2008) reports a record of one eating a froglet of another toad species.
Rio Grande leopard frog (*Lithobates berlandieri*)	Introduced. Possible predator of all life stages of LLFR. LCR MSCP (2016) and Sredl (2018) indicate uncertainty on whether this introduced species preys on LLFR. Brennan (2008) states: "Like other Arizona ranids, this species will eat a variety of invertebrate and vertebrate, aquatic and terrestrial prey…. If it continues to spread upstream in the Salt and Agua Fria drainages, it will likely prey upon and compete with native leopard frogs."
Sonoran lyre snake (*Trimorphodon lambda*)	Possible predator of LLFR juveniles and adults, given its dietary focus on small vertebrates in general, although it typically prefers dry ground (Brennan 2008).
Spiny softshell turtle (*Apalone spinifera*)	Possible predator of all life stages of LLFR—a generalized carnivore known to eat amphibians of all life stages (Brennan 2008; NatureServe 2018).
Western diamond-backed rattlesnake (*Crotalus atrox*)	Possible predator of LLFR adults—a generalized carnivore known to eat frogs (Brennan 2008).

Similarly, all of the terrestrial reptiles and adult stages of the amphibians found along the LCR and Bill Williams River valleys consume arthropods and other invertebrates. However, again, except for the Rio Grande leopard frog and American bullfrog, all these species are native to the region, and LLFR therefore likely co-evolved with them in ways that reduce competition. On the other hand, as noted above, the absence of LLFR from those portions of the LCR valley now occupied by the introduced Rio Grande leopard frog potentially results from competition between the two species as well as predation by the larger species on LLFR (LCR MSCP 2016).

HERBACEOUS VEGETATION

Full name: **The taxonomic composition, density, and spatial and temporal variability of the herbaceous aquatic and riparian vegetation assemblages at locations with or potentially suitable for LLFR habitat within the LCR ecosystem and their immediate surroundings**. As defined for this CEM (see "Definitions" immediately following the acronym list), the herbaceous vegetation layer in riparian communities along the LCR valley consists of vascular species 0.5 m or less in height.

Sredl et al. (1997a) and AZGFD surveys of potential LLFR habitat along the LCR and Bill Williams River valleys (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017) identify the herbaceous aquatic and riparian species that can occur at sites occupied by LLFR. Ground cover reported immediately surrounding LLFR habitat includes yerba-mansa (*Anemopsis californica*), canyon ragweed (*Ambrosia ambrosioides*), plantain (*Plantago* spp.), alkali sacaton (*Sporobolus airoides*), and arrowweed (*Tessaria sericea*). Herbaceous vegetation reported immediately along the perimeters of occupied pools and stream channels includes common reed (*Phragmites australis*), three-square bulrush (*Schoenoplectus americanus*) and other species of bulrush (*Schoenoplectus* spp.), spike rushes (*Eleocharis* spp.), and introduced Bermuda grass (*Cynodon dactylon*) and rabbitfoot grass (*Polypogon monspeliensis*). Herbaceous vegetation reported directly in or floating on the occupied pools and stream channels includes narrow-leafed cattail (*Typha angustifolia*) and other cattails (*Typha* spp.), duckweed (*Lemna* spp.), pondweeds (*Potomageton* spp.), and filamentous alga (*Cladophora* spp.). Studies of LLFR habitat elsewhere in Arizona (Wallace et al. 2010) have identified other grasses (*Muhlenbergia rigens*, *Cynodon dactylon*) and sedges (*Eleocharis* spp., *Carex* spp.) around the shores and another type of algae, *Chara* spp., in the water.

As discussed in chapter 3 (see "Resting/Hiding"), LLFR select locations for resting and breeding with greater aquatic vegetative cover immediately overhead, and greater canopy cover along the nearest shoreline, compared to surrounding aquatic-wetland site conditions (Cotten and Leavitt 2014; Leavitt et al. 2017).

Statistical findings confirm anecdotal records that LLFR select microhabitats for resting and breeding with emergent aquatic vegetative cover and nearby littoral canopy cover (AZGFD 2006; Sredl 2018; Swann and Wallace 2010). On the other hand, herbaceous vegetation at very high densities tends to exclude LLFR from using the affected sites. AZGFD surveys of locations with or potentially suitable for LLFR habitat and their immediate surroundings, not only along the LCR and Bill Williams River valleys but also along the Agua Fria and Verde River valleys to the east, specifically examined this relationship (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017). Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016) examined the characteristic of sites where LLFR were present, compared to surrounding conditions. Leavitt et al. (2017) studied sites used by LLFR specifically for breeding to examine the relationship between intensity of use (based on counts of egg masses) and site conditions including vegetation cover. These studies indicate that LLFR avoid sites with higher densities of emergent vegetation, and use sites for breeding less, the greater the density of emergent vegetation above some optimal range. The relict leopard frog has a similar pattern of habitat selection for resting and breeding, although it may select even more open habitat with less herbaceous or woody vegetation cover (Bradford et al. 2004, 2005; Harris 2006; Jaeger et al. 2010, 2014).

AZGFD authors of studies along the LCR, Bill Williams River, Agua Fria River, and Verde River valleys did not analyze their data to try to quantify an optimal range of emergent herbaceous vegetation densities for LLFR habitat or breeding site selection. However, Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014) identify those herbaceous species that, when present at high densities, specifically reduce habitat quality for LLFR, including cattail, bulrush, and common reed. Rosen et al. (2013) also recommend that habitat creation for native leopard frogs avoid fast-growing herbaceous species such as cattails and bulrushes because, without intensive management, they form dense stands that native leopard frogs tend to avoid.

As discussed in the LCR MSCP conceptual ecological models for other species (Braun 2018a, 2018b, 2018c), the aquatic macrophyte assemblage along the LCR valley has changed as a result of river regulation and introductions of non-native herbaceous species. The introduced herbaceous species include non-native varieties of common reed (Saltonstall 2002), which have contributed to a significant expansion of common reed throughout the LCR ecosystem.

A hybrid cattail species also may affect the LCR herbaceous vegetation assemblage. The species, *Typha x glauca*, is a hybrid of the native narrowleaf and broadleaf cattail (*T. angustifolia* and *T. latifolia*, respectively) or possibly sometimes a hybrid of broadleaf with the native southern cattail (i.e., with *T. domingensis*) (U.S. Department of Agriculture [USDA] 2018). Narrowleaf and hybrid cattails have similar habitat requirements and can grow in deeper water compared to broadleaf cattails (Motivans and Apfelbaum 1987). Both narrowleaf

and hybrid cattails aggressively out-compete broadleaf and southern cattails for habitat, not only by occupying deeper waters, but by establishing themselves in dense, mono-specific stands. Such stands can quickly dominate entire wetlands, eliminating open water and forming dense rhizome mats and litter, thereby crowding out other plants (Motivans and Apfelbaum 1987). Individual hybrid plants can produce as many as 700,000 fruits per year, and can reproduce asexually from their rhizomes, forming clones that can spread up to 8 m per year (Pennsylvania Department of Conservation and Natural Resources 2016). Aggressive expansion is more likely in disturbed wetlands, and hybridization exacerbates this potential. Disturbances that may trigger such aggressive expansion include changes in hydrology, wildfire suppression, or nutrient enrichment (Wilcox et al. 1984), common risk factors across the LCR ecosystem.

The USDA PLANTS Database (USDA 2018) currently does not identify any occurrences of hybrid cattails within the LCR ecosystem; however, this apparent absence may only reflect a pattern of misidentification resulting from the lack of systematic attention to the taxonomy of cattails along the LCR and difficulties in distinguishing between narrowleaf and hybrid cattails in the field (Pennsylvania Department of Conservation and Natural Resources 2016). All three parent *Typha* species occur in the LCR ecosystem, and hybridization occurs easily; therefore, it is likely that hybrid cattails are present.

Changes to the herbaceous vegetation assemblage in the LCR ecosystem involving cattails or common reed will have as yet unknown ecological consequences (McFarland et al. 2004; Rogalski and Skelly 2012). For example, overly dense stands of these aquatic macrophytes may suppress aquatic invertebrate abundance by reducing light and DO levels (National Invasive Species Information Center 2018), and they may reduce habitat availability for LLFR or other native species that avoid high densities of herbaceous aquatic vegetation. Conversely, different aquatic herbaceous species have different ranges of tolerance for variation in water chemistry, including the availability of nutrients; consequently, changes in water quality could affect aquatic herbaceous species assemblage composition and density (Finnegan 2013).

Aquatic herbaceous vegetation also affects hydrologic conditions through its effects on evapotranspiration and turbulence. Reclamation prepares annual reports on evapotranspiration and evaporation along the LCR valley (Reclamation 2014, 2018). These reports consistently indicate that the annual rate (in inches) of evapotranspiration from marsh vegetation (wetland area > 40% cattail, bulrush, and phragmites) exceeds the annual rate of evapotranspiration from open water by more than 10% between Davis and Parker Dams and by nearly 8% between Parker and Imperial Dams, while the rate from open water exceeds that from marsh areas by roughly 3 to 5% south of Imperial Dam (Reclamation 2018). The contrast between open-water and marsh evapotranspiration along the LCR valley is greater during the hottest months. The rate of evapotranspiration from marsh areas in June exceeds the rate from open water by nearly 40% above Parker Dam,

by nearly 30% between Parker and Imperial Dams, and by 15% below Imperial Dam (Reclamation 2018). Consequently, changes in the density of aquatic herbaceous vegetation could entail changes in hydrologic conditions, particularly during the hottest months (e.g., an increase in the density and/or extent of marsh vegetation could increase the rate at which pools shrink and stream flows decline as the weather becomes hotter between spring and summer, in the absence of stable replacement sources). Aquatic herbaceous vegetation also sustains its own habitat by slowing the movement of water (Fernandez and Madsen 2013), thereby also stabilizing substrates.

Herbaceous riparian and aquatic vegetation affects LLFR in five additional, more specific ways, as cover for larvae-juveniles and adults, as food and feeding surfaces for larvae, as habitat for potential prey for adult LLFR, as habitat for potential predators of all life stages of LLFR, and as surfaces to which adult female LLFR may attach their egg masses. Additionally, some characteristics of the herbaceous aquatic and riparian vegetation assemblages affect the effectiveness of VES methods for monitoring LLFR and, therefore, may affect understanding of LLFR habitat preferences. The following paragraphs discuss these six types of interactions, beginning with the effects on monitoring. (Herbaceous vegetation also affects LLFR indirectly in other ways [e.g., by affecting the fire regime, substrate, periphyton and POM in the water, and hydrology at locations with or potentially suitable for LLFR habitat], as noted briefly above and discussed elsewhere in this chapter).

Howland et al. (1997), in their investigations of the effectiveness of VES methods for monitoring Arizona ranid frogs in general, noted that lower densities of vegetation enhance the visibility of leopard frogs for VES detections, while higher densities impair it. They caution that vegetation density therefore may affect VES results. Similarly, AZGFD investigations along the LCR and Bill Williams River valleys (Cotten and Grandmaison 2013; Cotten and Leavitt 2014; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b) consistently report that the density of emergent vegetation at locations with or potentially suitable for LLFR habitat affected monitoring. Specifically, high densities of emergent vegetation impaired the ability of field teams to visually detect LLFR.

AZGFD teams surveying for LLFR in the LCR, Bill Williams River, Agua Fria River, and Verde River valleys (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Miller and Cotten 2016; Miller and Leavitt 2015; Leavitt et al. 2017; O'Donnell and Leavitt 2017a, 2017b; see chapter 4, "Monitoring, Capture, Handling") sought to compensate for the effects of high vegetation density (both herbaceous and woody) on the probability of detecting LLFR by the following methods:

- Using dip nets to attempt to capture LLFR in dense vegetation to confirm their presence (Rosen et al. 2013; Sredl et al. 1997b; Swann and Wallace 2010; Wallace et al. 2010).

- Taking more time to conduct VES monitoring in dense vegetation, including forcing transects through the vegetation.

- Supplementing VES efforts with an audio broadcast call/response component (VES C/R), funnel trap arrays (FTAs) left in place for 2 nights, environmental deoxyribonucleic acid (eDNA) sampling, and nighttime DAR sampling.

O'Donnell and Leavitt (2017b) report that VESs had the highest probability of detecting LLFR presence/absence in AZGFD field plots along the Bill Williams and Big Sandy River valleys. The study did not evaluate how the different methods (VES, VES C/R, FTA, eDNA sampling, and DAR) varied in their ability to assess LLFR abundance or in their ability to detect LLFR in dense versus sparse vegetation. However, the investigators noted that dense vegetation may reduce the transmission of sound, affecting the results of VES C/R and DAR monitoring, and that FTAs were particularly effective in detecting LLFR in dense vegetation.

Herbaceous aquatic vegetation in the LCR ecosystem, and litter produced by this vegetation, provides cover habitat for LLFR larvae-juveniles and adults. AZGFD (2006) summarizes several reports on LLFR habitat use as follows: "Shallow water with emergent and perimeter vegetation provides basking habitat and deep water, root masses, undercut banks, and debris piles provide refuge from predators and potential hibernacula." Sredl et al. (1997a) selected the six sites for their LLFR mark-recapture study in part because low densities of emergent and shoreline vegetation at these sites made them particularly suitable as LLFR habitat. (An increase in vegetation density at one site [Tule Spring] forced Sredl et al. (1997a) to drop it from the study because the site "… became too dense to allow thorough sampling of frogs."). Sartorius and Rosen (2000) report that LLFR also use *Cladophora* mats for concealment: "During periods of low discharge, pools had cyclical blooms of filamentous algae (*Cladophora*) that often covered the entire surface with a thick mat. When available, these algae mats (or organisms within them) were fed upon heavily by leopard frog larvae and also were used for concealment by larvae and adults."

As noted in chapter 2 and chapter 3, "Foraging," the diet of LLFR larvae likely includes submerged plant tissues, organic debris, and algae, including algae growing on the surfaces of submerged plant tissues. For example, as noted above, Sartorius and Rosen (2000) observed LLFR larvae hiding in and feeding "heavily" on mats of filamentous algae (*Cladophora*), including possibly on organisms within these mats. The literature does not include any more specific studies on the LLFR larval diet.

LLFR adults feed within the stands of herbaceous (and woody) vegetation that they also use for cover, except during inter-site movement (see chapter 3). The composition and density of the herbaceous vegetation in and immediately around sites occupied by LLFR presumably affect the types and abundance of arthropods and other invertebrates on which LLFR adults feed, including beetles, flies, terrestrial stages of aquatic invertebrates, spiders, earthworms, slugs, and snails (see chapter 3, "Foraging"). As noted in the discussion of LLFR foraging in chapter 2, the AZGFD (2006) reports that "[s]tomach analyses of other [adult] members of the leopard frog complex from the western United States show a wide variety of prey items, including many types of aquatic and terrestrial invertebrates (e.g., snails, spiders, insects) and vertebrates (e.g., fish, other anurans, small birds)." However, the literature does not address how the composition and density of the herbaceous vegetation in and immediately surrounding sites occupied by LLFR may affect LLFR adult foraging.

The composition and density of the herbaceous vegetation in and immediately surrounding sites occupied by LLFR necessarily also affects the types and abundance of species that may prey on LLFR eggs, larvae-juveniles, or adults. As noted above, this chapter (see "Birds and Mammals," "Fish and Herpetofauna," and "Macroinvertebrates") and chapter 3 (see "Predation)", the list of potential predators of LLFR along the LCR and Bill Williams River valleys consists of species that may live in or at least visit to feed in the pools, streams, and wetlands where LLFR occur. For example, Nadeau et al. (2011) found that the probability of Yuma clapper rail occupancy in restored marsh habitat positively correlated with low densities of bulrush and moderate densities of common reed and southern cattail. Vegetation conditions may also affect the local abundances of American bullfrog and crayfish (Cotten and Leavitt 2014). Rogalski and Skelly (2012) report a possible positive relationship between common reed expansion and non-native American bullfrog productivity. However, the literature on LLFR does not systematically address specifically how the composition and density of the herbaceous vegetation in and immediately surrounding sites occupied by LLFR may affect the composition, abundance, or foraging behaviors of the many species of birds, mammals, fishes, herpetofauna, or macroinvertebrates that may prey on LLFR at these sites.

Finally, LLFR females use submerged vegetation, particularly submerged herbaceous vegetation, as attachment surfaces during ovipositing (AZGFD 2006; Sredl 2018). AZGFD studies of LLFR breeding site selection patterns along the Bill Williams, Agua Fria, and Verde River valleys (Leavitt et al. 2017) provide additional information. Specifically, "… the majority of sites selected … for oviposition had [a] higher canopy than the randomly selected sites and were relatively close to cover and sites where they could crawl out of the water." Further, Leavitt et al. (2017) found that LLFR oviposited on the following plants (numbers = number of egg masses observed): "Unknown (25); rush (*Juncus* [*Schoenoplectus*] spp. and *Typha* spp. (15); tamarisk (*Tamarix* spp.) (9); willow (*Salix* spp.) (9); twig (2); cottonwood (*Populus* spp.) (1); leaf (1)." (This list

includes woody species, as discussed later in this chapter. LLFR also selected locations for ovipositing based on the availability of overhead canopy provided by woody vegetation, as also discussed later in this chapter.)

HYDROLOGIC REGIME

Full name: **The magnitude, timing, and duration of surface water availability and movement at locations with or potentially suitable for LLFR habitat within the LCR ecosystem and the patterns of variation in these over time**. This habitat element addresses features of the surface water hydrologic regime that may affect LLFR occupancy, behaviors, and life-stage outcomes at individual sites, including water permanence, depth, wetted area, movement (flow or turnover), and their temporal variability, including extreme events (droughts and floods). The following paragraphs discuss each of these five features (water permanence, depth, wetted area, movement, and temporal variability) in turn.

Most remaining populations of LLFR in Arizona are small and isolated (Sartorius and Rosen 2000; see discussion of genetic fragmentation in chapter 2, "LLFR Life Stage 3 – Adults). The literature consistently identifies losses of drainage network connectivity, both within and between watersheds across the historic range of LLFR, as a leading cause of the collapsing geographic distribution of LLFR and/or similar collapses among other ranid frogs of the Western United States (AZGFD 2006; Hayes and Jennings 1986; LCR MSCP 2016; Sredl 2018; Sredl et al. 1997b). The leading causes of drainage network fragmentation identified in this literature include direct habitat loss as a result of stream diversions and groundwater withdrawals that eliminate surface water flow, habitat destruction by severe sedimentation, and occupation of LLFR habitat by highly effective predators and/or competitors such as the American bullfrog. On the other hand, as discussed below (see "Hydrologic Regime"), LLFR evolved in adaptation to at least some natural hydrologic fragmentation (Sartorius and Rosen 2000; see chapter 1, "Lowland Leopard Frog Reproductive Ecology) to which at least some non-native predators may not be well adapted. As noted by Cotten and Grandmaison (2013), "The canyons of southeastern Arizona are under constant threat of drought and are frequently cut off from perennial water sources. Consequently, these arroyos and canyon pools may remain relatively free of predatory fishes and bullfrogs, which are less adapted to periods of drought and flood." Discussing specifically the reaches of the Bill Williams River below Alamo Dam occupied by LLFR, Cotten and Leavitt (2014) note, "Surface water becomes more ephemeral and often percolates into the sand near the Bill Williams River National Wildlife Refuge eastern boundary and onto Planet Ranch. This section has fewer predators and an abundance of small ephemeral pools ideal for amphibian breeding."

The literature consistently reports that LLFR occupy locations with standing or flowing water present either permanently (perennially) or during at least the spring breeding season. However, descriptions of LLFR habitat with only semi-permanent surface water also imply that these locations have water not only during spring but also during fall and winter. In contrast, LLFR do not occupy ephemeral pools fed only by direct rainfall; rather, they only occupy locations along flow channels and their adjacent floodplains, even if these locations are only seasonal pools (Sartorius and Rosen 2000; Sredl et al. 1997a; Swann and Wallace 2010; Wallace et al. 2010; Zylstra et al. 2015).

As discussed above (see "Drainage Network Connectivity"), LLFR evolved in a landscape characterized by at least episodic natural hydrologic fragmentation (Sartorius and Rosen 2000; chapter 1, "Lowland Leopard Frog Reproductive Ecology). As noted by Cotten and Grandmaison (2013), "The canyons of southeastern Arizona are under constant threat of drought and are frequently cut off from perennial water sources." Discussing specifically the reaches of the Bill Williams River below Alamo Dam occupied by LLFR, Cotten and Leavitt (2014) note, "Surface water becomes more ephemeral and often percolates into the sand near the Bill Williams River National Wildlife Refuge eastern boundary and onto Planet Ranch. This section has fewer predators and an abundance of small ephemeral pools ideal for amphibian breeding."

Otherwise, hydrologically, LLFR are habitat generalists: They may occupy natural features such as the shallows of rivers and permanent streams, side-channel and off-channel wetlands along river and permanent stream floodplains, permanent pools in intermittent streams, beaver ponds, cienegas, and springs; and artificial features such as earthen cattle tanks, livestock drinkers, canals, irrigation sloughs, wells, mine adits, abandoned swimming pools, and ornamental backyard ponds (Sredl 2018). Earthen cattle tanks, constructed specifically to impound and maintain permanent surface water for cattle along drainage channels are not only attractive to LLFR but may be amenable to management to benefit both cattle and native frogs (Howland et al. 1997; Rosen et al. 2013; Sredl et al. 1997a).

LLFR adults survive the loss of surface water at a location by moving to another site (see chapter 3, "Occupancy and Inter-Site Movement"), or finding refuge in mud cracks, mammal burrows, or rock fissures (see chapter 3, "Resting/Hiding"), and may quickly reoccupy a location when water returns (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014; Sredl et al. 1997a). The literature does not report how long LLFR adults may survive in mud cracks, mammal burrows, or rock fissures during an absence of surface water at a site.

Their non-use of ephemeral, rainfall-dependent pools distinguishes LLFR from the Colorado River toad (Cotten and Leavitt 2014, 2016; this chapter, "Fish and Herpetofauna; chapter 3, "Competition")—a possible example of resource partitioning. On the other hand, both the American bullfrog and northern crayfish prefer permanent, stable water bodies, a factor often cited as a possible

explanation for the disappearance of LLFR from many permanent water bodies and their relegation mostly to semipermanent waters or waters with permanent but highly variable water availability (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014; Rosen et al. 2013; Sartorius and Rosen 2000; also see below).

LLFR select locations both specifically for breeding and generally for occupancy based in part on water depth. However, investigators have quantified the pattern of selection only for breeding. Sartorius and Rosen (2000) found LLFR egg masses in their study area (a canyon near Tucson, Arizona) at depths up to 1 m beneath the surface but more often within 2 cm of the surface and occasionally slightly emergent at the water surface. Leavitt et al. (2017) found LLFR egg masses along the Bill Williams River and within the Agua Fria and Verde River watersheds of central Arizona with their tops an average of 3.27 ± 0.56 cm below the water surface and their bottoms an average of 5.85 ± 0.90 cm above the bottom of the water column. Leavitt et al. (2017) further report that the overall water depths at locations selected by LLFR for ovipositing were statistically significantly shallower than the depths at randomly selected control locations nearby—an average depth of 10.93 ± 1.91 cm at ovipositing sites versus 20.11 ± 4.7 cm at control sites ($t = 1.81$, $p = 0.07$).[7]

AZGFD studies of overall LLFR habitat preferences along the LCR and Bill Williams River valleys (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016) compared the water depths in 10 x 10 m plots at locations occupied by LLFR to the depths in plots at nearby control locations. The results indicate that LLFR were more abundant in shallower, more heavily vegetated flowing waters such as shallow-braided stream reaches. However, the AZGFD studies do not report the ranges of depths observed in occupied versus control plots, reporting the results only in terms of the strength of overall regression relationships.

Cotten (2011) and colleagues (Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016) attribute the observed spatial distribution of LLFR occupancy along the Bill Williams River Valley to LLFR avoidance of predators. However, areas with few or no LLFR could be areas the species avoids or areas in which predation has taken a particularly strong toll. Cotten and Leavitt (2014) specifically conclude: "Deep water allows for the persistence of large predators that, in addition to smaller predators such as crayfish, have been shown to be

[7] Leavitt et al. (2017) also report that LLFR egg masses recorded during their study averaged 5.58 cm thick (top to bottom). If the average depth of LLFR egg mass tops from the water surface and the average distance of LLFR egg mass bottoms to the substrate vary independently, this might suggest an average total water depth of 14.70 cm at the locations selected for ovipositing. However, Leavitt et al. (2017) in fact report an average total water depth of 10.93 cm at these locations. Such a result suggests that the average depth of LLFR egg mass tops from the water surface and the average distance of LLFR egg mass bottoms to the substrate do not vary independently.

detrimental to amphibians in prior studies … Much of the main stem LCR has been modified to discourage … shallow open side channels and braids. Outside of the Bill Williams River National Wildlife Refuge, Planet Ranch, and upstream sections of the Bill Williams River, habitat with dynamic shallow back waters has not been seen. The other refuges on the main stem LCR have the capacity to support restoration areas analogous to the habitat described in this analysis, but intensive anti-predator management techniques will be required to knock exotic species out of established habitats. The phenomenon of American bullfrogs not surviving on the Bill Williams River plays a key role in the persistence of lowland leopard frogs."

The AZGFD results also indicate that the mere presence of deeper waters nearby does not deter LLFR from occupying a location with suitable shallow water habitat. Other studies similarly have found LLFR occupying the shallow peripheries of water bodies such as cattle tanks and natural pools even when the maximum depths of the water bodies exceed the ranges of interest to LLFR for breeding (Sredl et al. 1997a; Wallace et al. 2010).

The literature does not clearly indicate whether the total area of shallow water habitat of suitable depth available at a site affects the minimum or maximum abundance of LLFR to be found at the site. Wallace et al. (2010) found more LLFR at larger pools in their study area, but they measured pool size in terms of volume rather than area of shallow-water habitat. Both Sredl et al. (1997a) and Sartorius and Rosen (2000) found that the surface area of an individual occupied pool could vary greatly over the course of a single year. Sredl et al. (1997a) reported that "At the beginning of our study at [Big Spring], total surface area of pools measured approximately 200 m^2. In the summer of 1992, one or more high-flow events reduced pool surface area to 35 m^2. Even though these flow events were strong enough to fill the main breeding pool with gravel, survivorship of adults and juveniles did not appear to be affected." Sartorius and Rosen (2000) similarly continued to find LLFR in permanent pools even after they had shrunk to 3–5 square meters (m^2). Sredl et al. (1997a) (also see Howland et al. 1997) also found that year-to-year abundance varied with pool size at individual sites and noted that the causes of the changes in pool size included drying from a drought and filling with sediment from a flood.

Seim and Sredl (1994 *in* AZGFD 2006) "… studied the association between [LLFR] juveniles and adult stages and pool size and found juveniles were more frequently associated with small pools and marshy areas while adults were more frequently associated with large pools." Since LLFR juveniles cannot move themselves between disconnected ponds, the pattern observed by Seim and Sredl (1994 *in* AZGFD 2006) could reflect a lower rate of survival of juveniles in larger pools. For example, juveniles of the closely related Chiricahua leopard frog are more active during the day, while adults of that species are more active at night (Jennings 1988), a difference that could result in a difference in predation patterns. However, no studies have formally examined the ecological differences

between LLFR juveniles and adults. Consequently, the difference in juvenile versus adult abundance in relation to pool size identified by Seim and Sredl (1994 *in* AZGFD 2006) remains unexplained.

The wetted area may affect opportunities for species that may prey on or compete with LLFR. Cotten and Leavitt (2014) (also see Cotten 2011; Cotten and Grandmaison 2013) took wetted area into account when they designed their survey of LLFR occupied and potential habitat along the LCR and Bill Williams River valleys, based on an expected greater abundance of predators in larger water bodies. "Backwaters along the main stem LCR that were greater than 5 acres in size were not surveyed due to the high probability of introduced non-native predatory fishes and American bullfrogs …, which prey upon and compete with native ranids." Rosen et al. (2013) similarly note that locations with larger quantities of habitat are more difficult to manage for restoring native frog populations because of greater opportunities for invasive species at larger sites.

High-flow events may inundate floodplain depressions, creating at least seasonal LLFR habitat (Sartorius and Rosen 2000). LLFR also may tolerate episodic flooding in situ (see below); however, they do not select settings with high-velocity base flows for occupancy or breeding. Instead, the literature reports that, in lotic waters, LLFR select for "moderate" or "low" flow velocities, which also tend to be settings away from main channels with their deeper water and higher base flow velocities (Cotten and Leavitt 2014; Sartorius and Rosen 2000). AZGFD studies of LLFR habitat selection in general along the Bill Williams River Valley (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014) and LLFR ovipositing site selection, in particular along the Bill Williams, Agua Fria, and Verde River valleys (Leavitt et al. 2017), found a consistent pattern of LLFR selection for lower rates of flow. However, none of these studies quantitatively report the ranges of discharge or flow velocity observed, either for LLFR habitat alone or in comparisons of LLFR habitat with nearby control locations. The literature thus does not quantify the upper limits of base flow velocity or discharge preferred or tolerated by LLFR for occupancy or breeding.

LLFR use of non-flowing waters such as cattle tanks and disconnected pools along otherwise dried channels indicate that LLFR may have no lower limit to the flow velocity or discharge they prefer or tolerate for occupancy or breeding. Sartorius and Rosen (2000) specifically note that LLFR can occupy pools that sustain mats of algae because they have little water movement. As noted, LLFR adults also may cope with a complete loss of surface water at a site by moving away or finding refuge underground. On the other hand, pools without turnover or fresh inflows can become hazardous to LLFR before drying completely due to lowered DO concentrations, increasing salinity due to evaporation, or other interactions. Sredl et al. (1997a), for example, describe a frog die-off at one cattle tank in 1994: "We suspect that a high detritus load in the pond, coupled with lowering of water level, high water temperature, and low concentrations of DO, combined to form an anoxic environment suitable for proliferation of sulphur

producing bacteria. This event reduced a population of 60–80 adult frogs to fewer than 10."

LLFR have evolved adaptations not only to specific conditions of water permanence, depth, and flow but also to the high temporal variability in these features that characterizes the Southwest United States. As Sartorius and Rosen (2000) summarize, precipitation and runoff across the historic range of LLFR:

> *… follows the bimodal Sonoran pattern … with peaks in summer (July – August) and winter (December – January) separated by a highly predictable foresummer drought …. Summer storms tend to be localized and strong and often cause flash floods in small drainages. Winter rains are characteristically widespread and more prolonged, producing long periods of high stream discharge in wet years rather than the brief, unpredictable, scouring spates seen in summer. Presence of stable, flowing water in the stream is most predictable during late winter to early spring; and less so during summer, when prolongation of the summer dry period may lead to habitat drying, or onset of summer thunderstorms often produce flash floods.*

The region also experiences significant year-to-year variation in the magnitude and timing of rainfall both regionwide and between localities within the region. Air temperatures and associated evapotranspiration are somewhat more consistent from year to year and across the region, following a unimodal pattern with a prolonged summer peak. The rate of evapotranspiration from a water body and its surrounding vegetation determines how quickly the water dries down following each input of fresh water.

Sartorius and Rosen (2000) summarize the reproductive ecology of LLFR in this predictably variable hydrologic setting:

> *Eggs hatch primarily in late March with a few lasting as late as May. Water levels in perennial pools usually begin to drop in mid-May and reach seasonal lows just before the onset of summer rains, usually in early July. Thus, mobile tadpoles or metamorphs and not immobile egg masses, are exposed to the summer drought. Egg masses are absent also from the summer flash flooding season in late July through early September. Floods would undoubtedly wash egg masses downstream into unsuitable low desert habitats that quickly dry after storms. Summer rains also provide a potential dispersal opportunity for metamorphs. Tadpoles that hatch in spring enjoy a warm and food-rich summer and grow rapidly to metamorphosis, or at least to a size at which they can survive moderate summer flooding. Tadpoles that hatch in fall may share some of the benefits of spring hatchlings, including avoidance of summer drought and late summer flood scour.*

The LLFR adaptation to this predictably variable hydrologic setting thus includes breeding without the need for cues from precipitation, and may also include some plasticity in larval development, resulting in faster larval development under

drying conditions. Sartorius and Rosen (2000) report that they "… re-surveyed [their study location] on 25 June 1996 at the height of a protracted summer drought episode when it was already reduced to four small pools. We counted 5 adult, 188 metamorphic, and 62 pre-metamorphic *R. yavapaiensis*. Larval development and transformation were thus slightly advanced in this relatively drier year."

The LLFR adaptation to this predictably variable hydrologic setting also includes abilities to disperse downstream as juveniles and adults in runoff pulses, move overland to another site as adults (see chapter 3, "Occupancy and Inter-Site Movement") find refuge in mud cracks, mammal burrows, or rock fissures (see chapter 3, "Resting/Hiding"), quickly reoccupy a location when water returns, and reproduce in large numbers (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014;Sartorius and Rosen 2000; Sredl 2018; Sredl et al. 1997a; Swann and Wallace 2010; Wallace et al. 2010; also see chapter 1). These abilities result in a high level of variability in LLFR occupancy and abundance within and between watersheds (Rosen et al. 2013; Sredl et al. 1997a, 1997b; Wallace et al. 2010).

The literature does not document how much drying must occur at an occupied water body to trigger emigration; however, waters with higher initial salinities may become uninhabitable sooner during drying (i.e., before drying out completely): Evapotranspiration concentrates dissolved salts in the remaining water, and LLFR have a low tolerance for salinity (see chapter 3, "Chemical Stress," and this chapter, "Water Chemistry"). Further, as Howland et al. (1997) note, "Unlike many other anurans of the desert southwest, leopard frogs are obligate wetland species …. They lack adaptations that allow others to endure long periods of drought."

Additionally, the LLFR adaptation to its predictably variable hydrologic setting appears to provide advantages in reducing opportunities for contacts with predators, both native and exotic, and possibly also with competitors. Numerous investigators (AZGFD 2006; Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014; Rosen et al. 2013; Sartorius and Rosen 2000; Sredl 2018; Sredl et al. 1997a) have noted that the non-native American bullfrog and northern crayfish and many non-native piscivorous fishes do not tolerate the wide range of fluctuating flow rates that LLFR tolerate so readily. Consequently, these potential predators do not occur in LLFR habitat that experiences such fluctuations. For example, Rosen et al. (2013) state: "In lower Cienega Creek, in the County Preserve, bullfrogs were first observed during the late 1990's, having colonized from golf course ponds downstream at Vail; but they have never bred or become established in the strongly scouring desert stream flood regime of the creek there." Cotten and Grandmaison (2013) also note that high beaver activity can contribute to variability in flooding patterns, as they observed along the Bill Williams River.

In turn, the timing of higher summer flows may reduce competition between LLFR and the Colorado River toad. Cotten and Leavitt (2016) (also see Cotten and Grandmaison 2013; Cotten and Leavitt 2014) note that "… low flows of the Bill Williams River from Alamo Dam may also contribute to a lack of [Colorado River toad] breeding habitat …. Higher flows in the [Bill Williams River] may create more isolated pools adjacent to the river after monsoon floods suitable for Colorado River toad breeding." O'Donnell and Leavitt (2017a) (also see O'Donnell and Leavitt 2017b) also note that "… the breeding window and calling window of lowland leopard frogs is much larger [than that for the Colorado River toad] and not dependent on isolated weather events."

Finally, fluctuating flows at LLFR sites can also affect monitoring. O'Donnell and Leavitt (2017a, 2017b) note that, on one occasion, a flood destroyed or displaced DAR equipment along the Big Sandy River.

INFECTIOUS AGENTS

Full name: **The species, abundances, spatial and temporal distributions, and activity levels of infectious agents to which LLFR are susceptible at locations with or potentially suitable for LLFR habitat within the LCR ecosystem**. As noted in chapter 3 (see "Disease"), LLFR in all life stage are likely subject to infection by many viral, bacterial, fungal, and parasitic agents, as are all frogs and other amphibians (Duellman and Trueb 1986). Non-lethal infections may make the affected individuals vulnerable to mortality from other causes, and other sources of stress correspondingly may increase susceptibility to disease (Blaustein et al. 2003; Davidson et al. 2002).

Reviews of the decline of leopard frogs generally in the Western United States or LLFR in particular consistently identify disease from pathogens and parasites as likely factors in temporary extirpations at single sites up to extended disappearances at larger geographic scales (AZGFD 2006; Blaustein et al. 2003; Davidson et al. 2002; Hayes and Jennings 1986; LCR MSCP 2016; Sredl 2018; Sredl et al. 1997a). The literature identifies three individual infectious agents or classes of such agents affecting LLFR:

- Goldberg et al. (1998) identified numerous parasitic trematodes (helminth) in the gastrointestinal tracts, lungs, urinary bladders, and body cavities LLFR, Chiricahua leopard frogs, and American bullfrogs in Arizona. As noted in chapter 3 (see "Disease"), the study did not attempt to quantify the magnitude of effects LLFR may experience from this burden of infection.

- Sredl et al. (1997a) report two outbreaks in LLFR of the bacterium (*Aeromonas hydrophila*), resulting in frog septicemia or "red-leg," a common amphibian disease. The outbreaks resulted in local extirpations. Hayes and Jennings (1986) identify *A. hydrophila* as a possible cause of localized extirpations of western ranid frogs but also note that "… the influence of septicemia-associated bacteria on wild ranid populations is controversial." Sredl et al. (1997a) note that the outbreaks in LLFR followed cold-weather events, possibly indicating that the thermal stress may have contributed to the magnitude of the bacterial outbreak. As noted elsewhere in this CEM, frogs in general are readily susceptible to such synergistic interactions among stressors (Blaustein et al. 2003). Stress due to the presence of chemically harmful conditions may also increase the possibility of an outbreak (Sredl et al. 1997a).

- As discussed in chapter 3, "Disease," a growing body of studies documents infestations of LLFR and closely related species by *Bd*, resulting in outbreaks of chytridiomycosis (*aka* chytrid fungal disease) with high rates of mortality (see Bradley et al. 2002; Jaeger et al. 2016, 2017; Rosen et al. 2013; Savage and Zamudio 2011, 2016; Savage et al. 2015; also see discussions in LCR MSCP 2016 and Sredl 2018). These outbreaks also may coincide with cold-weather events; however, in this case, the reason may be simply that *Bd* itself is more active under cooler conditions and loses most of its infectious abilities above 25 °C and especially above 28 °C (Bradley et al. 2002; Jaeger et al. 2016). Outbreaks among leopard frogs of the Southwestern United States occur overwhelmingly during cold winter weather, and populations in geothermal springs with warm temperatures year round appear unaffected (Bradley et al. 2002; Jaeger et al. 2016; LCR MSCP 2016; Rosen et al. 2013; Sredl 2018). Bathing LLFR adults in warmer water similarly may help them shed or avoid being infected by *Bd* (Rosen et al. 2013).

However, no studies have been conducted to investigate the overall body load of infectious agents and its variation among LLFR. Other than for *Bd*, no further studies have been conducted to systematically look for possible synergistic interactions between disease and other sources of stress in LLFR or closely related species.

MACROINVERTEBRATES

Full name: **The taxonomic, functional, size composition, abundances, and activity levels of the macroinvertebrate assemblage that may interact with LLFR or its habitat along the LCR valley, and spatial and temporal variation in these properties**. Ohmart et al. (1988) catalog the high diversity of terrestrial, flying, and aquatic macroinvertebrates that may occur along the

LCR valley, including the aquatic larvae of terrestrial and flying species. Macroinvertebrates may be food items for LLFR adults, predators of LLFR in all life stages, or competitors with LLFR larvae for food or habitat, and they may affect habitat conditions that in turn affect LLFR. The presence of non-native crayfish potentially also could affect LLFR embryo development. The following paragraphs discuss these possible interactions.

As noted in chapter 2 and chapter 3 (see "Foraging"), LLFR adults reportedly prey almost exclusively on terrestrial and flying macroinvertebrates, including beetles, flies, the terrestrial life stages of aquatic invertebrates, spiders, earthworms, slugs, and snails. However, no studies specifically have focused on the LLFR adult diet or foraging behaviors (LCR MSCP 2016).

The major species accounts for LLFR (AZGFD 2006; LCR MSCP 2016; Sredl 2018) report that predators of LLFR larvae include several types of insects, notably giant water bugs (Belostomatids), backswimmers (Notonectids), predaceous diving beetles (Dytiscids), and the aquatic larvae (nymphs) of dragonflies (Anisopterans). These reports appear to be based on observations of these taxa in general rather than observations of their feeding on LLFR in particular. The literature also includes numerous reports of the northern crayfish and possibly also the red swamp crayfish as predators of LLFR of all life stages (see chapter 2 and chapter 3, "Predation"). Many of the aquatic and terrestrial macroinvertebrates cataloged by Ohmart et al. (1988) along the LCR valley are carnivorous in one or more of their life stages and can reach sizes capable of attacking vertebrates in the size range of LLFR adults. However, the literature does not contain any studies specifically focused on predation by invertebrates on LLFR of any life stage (LCR MSCP 2016).

Some of the aquatic macroinvertebrates cataloged by Ohmart et al. (1988) for the LCR valley are herbivorous and, therefore, potentially could compete with LLFR larvae for food. No studies have been conducted to investigate competition between aquatic macroinvertebrates and LLFR larvae (LCR MSCP 2016).

The northern crayfish not only preys on LLFR and other amphibians (and small fishes) in the Southwestern United States, but it also modifies habitat in ways that may exclude LLFR and related species. Specifically, crayfish reduce aquatic vegetation and cover for frogs in general (Fernandez and Rosen 1996; Rosen et al. 2013; Witte et al. 2008).

Finally, Saenz et al. (2003), in a study of the effects of a different species of crayfish (*Procambarus nigrocinctus*) on the southern leopard frog (*Rana = Lithobates sphenocephalus*) native to the Southeastern United States, found that the non-lethal presence of crayfish (caged with no access to eggs) induced

accelerated hatching of frog embryos. No studies have been conducted to investigate whether this relationship might also hold for the interaction of non-native crayfishes with LLFR.

MONITORING, CAPTURE, HANDLING

Full name: **The methods, frequencies, timing, and duration of (a) monitoring of LLFR habitat and (b) monitoring, capture, and handling of LLFR during field investigations**. Including this habitat element in a CEM makes it possible to represent ways in which monitoring, capture, or handling may affect the subject species and, conversely, which particular characteristics of the species or its habitat may affect its monitoring.

The literature on LLFR contains several discussions of methods for monitoring LLFR in the field. Sredl et al. (1997a) discuss their use of mark-recapture methods to assess LLFR abundance and population dynamics. Howland et al. (1997) discuss and evaluate the effectiveness of VESs for Arizona leopard frogs in general at the same sites studied by Sredl et al. (1997a). Sredl et al. (1997b) report on the results of VESs statewide in Arizona for ranid frogs and other riparian amphibians and reptiles. These three studies supplemented their VESs with the use of dip nets to capture individuals for further identification. Sartorius and Rosen (2000) present the results of a study using VESs specifically for LLFR along transects in a small study area near Tucson, Arizona, during which they tried to avoid handling LLFR beyond the minimum needed to permit initial identification (see below). Parker (2006), Swann and Wallace (2010), and Wallace et al. (2010) summarize the results of VESs in the Rincon Mountains in Saguaro National Park around Tucson. Rosen et al. (2013) similarly report the use of VESs to assess the distribution of Arizona leopard frogs in southeastern Arizona, also supplemented with dip netting and seining to capture individuals for further identification.

The AZGFD (Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b) evaluated the relative effectiveness of several field survey methods to assess LLFR and Colorado river toad presence/absence distributions along the LCR and Bill Williams River valleys (O'Donnell and Leavitt 2017b). The AZGFD specifically evaluated five survey methods to assess LLFR presence/absence during the spring breeding season: (1) VESs, (2) VES C/Rs, (3) FTAs left in place for 2 nights, (4) eDNA sampling, and (5) nighttime DAR recordings. Sampling for eDNA proved to have a higher detection for the presence of LLFR than any other method, but it also a higher cost per detection. VESs proved to be the most cost-effective method for surveying for LLFR presence/absence, especially when combined with the audio broadcast call/response component (VES C/R).

The aforementioned surveys to detect LLFR presence/absence differ in the time(s) of day during which they took place, although not all reports specify the time of day when the surveys were carried out. Sredl et al. (1997b) state that they mostly surveyed "… during the daytime, between dawn and dusk." Sartorius and Rosen (2000) surveyed "between 0900 and 1600 h." Rosen et al. (2013) surveyed "… during daylight hours and at night, and localities with potential frog habitat that did not yield observations as expected during daylight were usually revisited at night." The methods tested by the AZGFD, as summarized by O'Donnell and Leavitt (2017b), specifically involved nighttime VESs, nighttime VES C/Rs, FTAs left in place for 2 nights and the intervening day, and nighttime DAR recording. The AZGFD also tested and recommended including daylight VESs for tadpoles, young frogs, or egg masses to confirm successful breeding activity. O'Donnell and Leavitt (2017b) note that "[g]enerally, VESs are conducted during the night because lowland leopard frogs are easier to detect then, but that may not be when they are most active." In turn, they note that FTAs have the ability to capture individuals at all hours of the day and night and so provide data on times of the day when LLFR may be more active but missed by other methods such as VESs.

The AZGFD (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017) also has carried out surveys of habitat historically or currently occupied by LLFR along the LCR, Bill Williams, Big Sandy, Agua Fria, and Verde River valleys to assess LLFR habitat requirements and identify habitat potentially suitable for LLFR reintroduction. These studies involved two phases: First, surveys along the LCR and Bill Williams River took place "… during daylight and at night looking for adult frogs or listening for calling frogs" (Leavitt et al. 2017). Second, within a fixed, brief period following the initial survey, field crews returned to all occupied sites to collect data on habitat conditions both immediately within and surrounding each occupied site. The crews also collected data on the same habitat variables at randomly selected locations nearby, for comparison. The surveys by Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016) examined all sites found to be occupied by LLFR. The surveys conducted by Leavitt et al. (2017) examined only sites found to have LLFR egg masses during the initial survey. The two groups of studies also used slightly different methods to inventory habitat conditions within and around each occupied site.

Species of conservation concern may be sensitive to disturbance by field investigations, not only by the intrusion of field crews but by specific activities (such as those resulting in capture) and by handling following capture. Movements of field investigators and their equipment between sites also can transfer infectious agents and potentially harmful chemicals (including hand cleaners and lotions, insect sprays, or sunscreen) between sites unless the investigators take adequate precautions to prevent this (Graeter et al. 2013).

Sredl (2018) notes that surveys do disrupt LLFR adults, stating that, when surveying for LLFR, field investigators may cause "… 10–20 frogs [to] jump with each step along the shoreline." Field investigations of LLFR generally intentionally take steps to minimize any stress to LLFR. Sartorius and Rosen (2000) state that they sought to minimize the possibility of causing stress to LLFR at their study sites by avoiding pursuing, capturing, or handling the frogs "… beyond what was necessary for initial identification." O'Donnell and Leavitt (2017a; also see Miller and Cotten 2016) mention that "… DARs have an added benefit of reduced disturbance to the target species during calling and the ability to retain a saved recording for further analysis." However, the aforementioned AZGFD studies did not directly evaluate any possible effects of the studied methods on LLFR. The lack of data on embryo numbers in LLFR egg masses may also reflect care by field investigators to avoid disturbing egg masses altogether. Otherwise, the literature on LLFR does not systematically examine whether survey methods affect LLFR eggs, larvae, adults, or breeding activity.

PERIPHYTON AND PARTICULATE ORGANIC MATTER (POM)

Full name: **The taxonomic composition, size, density, and nutritional quality of the periphyton and POM in the water column, and resting on substrates, at locations with or potentially suitable for LLFR habitat within the LCR ecosystem, and spatial and temporal variation in these properties**. This habitat element focuses on two broad classes of aquatic life and organic matter: (1) the periphyton community living on the mineral substrates, submerged plant parts, and submerged coarse plant litter at locations with or potentially suitable for LLFR habitat and (2) the POM in the water and that which settled to the bottom at these locations. POM consists of microscopic organisms (including phytoplankton and zooplankton), fine plant litter, and other fine organic matter either produced within and immediately surrounding a given water body or washed in from upstream and surrounding terrestrial communities.

As discussed in chapter 2 and chapter 3, "Foraging," LLFR larvae are herbivorous and described as feeding specifically on algae, organic debris, plant tissue, and micro-organisms. However, as also noted above (see chapter 3, "Foraging"), this description of LLFR larval foraging in fact rests on only two sources—a single, unpublished report from southeastern Arizona (Marti and Fisher 1998) and a single short comment in a larger report by Sartorius and Rosen (2000). Sredl and Jennings (2018) report that the unpublished study by Marti and Fisher (1998) found the following potential food items and browsing surfaces for larvae of both LLFR and Chiricahua leopard frogs at the study site in southeastern Arizona: "… bacteria, diatoms, phytoplankton, filamentous green algae, water milfoil (*Myriophyllum* spp.), duckweed (*Lemna minor*), and detritus." Sartorius and

Rosen (2000) describe LLFR larvae feeding on filamentous algae mats and small organisms within them, and they also note that LLFR larvae hatching in September or October "… face lower temperatures *and reduced primary productivity*, which prolong larval development and extend exposure to predation, fall and winter drought, and cold floods in late winter" [emphasis added].

The literature reviewed for this CEM does not provide any other information on how the availability of periphyton and POM, due to environmental/seasonal conditions, may affect LLFR larvae or what factors may affect this availability other than competition (see chapter 3). Additionally, the production of periphyton and POM in freshwater ecosystems are key components of primary productivity, which generally varies with water temperature and clarity and the availability of sunlight and inorganic nutrients such as soluble ions of nitrogen and phosphorus (Allan and Castillo 2007). No studies have been conducted to examine the effects of variation in primary productivity on habitat suitability for LLFR larvae.

Periphyton and POM potentially may interact with LLFR in other ways, not simply as food for LLFR larvae. Pinder and Friet (1994) found that the egg masses of some amphibians harbor algae, the oxygen generated by which supplements the diffusion of this crucial gas to the developing embryos from the surrounding water. However, no study has examined the possibility of this kind of interaction in LLFR or any closely related frog species.

The EPA (2016), Hamilton (2003, 2004), Presser and Luoma (2006), and others note that selenium in freshwater ecosystems cycles through multiple ecological compartments. These compartments include not only surface and groundwater but also the organic matter in the substrate, periphyton, and POM. Bioaccumulation of selenium in larger organisms occurs through their consumption of these types of organic matter or consumption of other organisms that feed on this biomass. The bioaccumulation of mercury in freshwater food webs follows a similar set of pathways (Bank et al. 2007; Hinck et al. 2007, 2009; Patiño et al. 2012; Walters et al. 2015). However, no study has been conducted to specifically examine the ways in which these interactions could affect the possibility of selenium or mercury bioaccumulation in LLFR larvae or adults.

Finally, other habitat elements may affect the availability of periphyton and POM at locations with or otherwise potentially suitable for LLFR habitat. Axelsson et al. (1997), studying general effects of crayfish on frog larvae, found that grazing by crayfish can reduce the quantity and quality of periphyton and larger algae available as food and cover for frog larvae. These interactions compound the effects of predation by crayfish on frog larvae. As noted in this chapter, "Macroinvertebrates," studies in the Southwestern United States show that crayfish reduce aquatic vegetation and cover for the native frogs of the region in general (Fernandez and Rosen 1996; Rosen et al. 2013; Witte et al. 2008).

SUBSTRATE

Full name: **The types (texture) and stability of the substrate at locations with or potentially suitable for LLFR habitat within the LCR ecosystem and spatial and temporal variation in these features**. This element refers to the particle size distribution of the benthic sediment at locations with or potentially suitable for LLFR habitat and the frequency and magnitude of substrate movement, erosion (scour), and deposition (burial). These features may affect the suitability of individual locations for LLFR during different life stages, as well as for species that may prey on or compete with LLFR, and may affect or be affected by other habitat elements such as herbaceous vegetation and aspects of the hydrologic regime.

Sartorius and Rosen (2000) state that LLFR attach their eggs to "… vegetation, bedrock, or gravel." Otherwise, LLFR do not appear to select among sites or locations within sites based on substrate texture. Sredl et al. (1997a) note that one of the sites included in their mark-recapture study of LLFR (Alamo Canyon, southeastern Arizona) consisted of bedrock pools (tinajas) regularly scoured by surface runoff. Wallace et al. (2010) compared pools, including tinajas inhabited by LLFR along canyons in southeastern Arizona, to uninhabited pools in the same canyons to identify similarities and differences in pool substrate. They recorded the percentages of three categories of substrate in these pools: bedrock, boulder and cobble, and gravel and sand. The inhabited pools averaged 57.8, 5.2, and 37.0%, respectively, for these three categories – values that were statistically indistinguishable from the averages for the uninhabited pools. Cotten and Leavitt (2014) compared plots in locations occupied versus not occupied by LLFR along the Bill Williams River based on the presence versus absence of sand, gravel, cobble, and/or mud or silt. Nothing about substrate type proved statistically associated with occupied versus unoccupied locations. Finally, Leavitt et al. (2017) looked at the same four substrate types coded by Cotten and Leavitt (2014) plus bedrock in their study of LLFR breeding locations along the Bill Williams, Agua Fria, and Verde Rivers. They found the following dominant substrate type at 72 breeding sites: sand (41 sites), mud/silt (15 sites), gravel (2 sites), boulder (2 sites), cobble (1 site), and bedrock (1 site). Leavitt et al. (2017) compared these incidences to conditions at control sites and found no statistical difference.

The difference in incidence of bedrock at sites used by LLFR in the canyons of southeastern Arizona and along the Bill Williams, Agua Fria, and Verde Rivers in central and western Arizona presumably reflect differences in geology between canyon (southeastern Arizona) and floodplain (Bill Williams, Agua Fria, and Verde River valleys) settings that do not affect LLFR. Outside of pools with bedrock as the dominant substrate, the results across these diverse settings indicate a preference for more sand and silt and less cobble and boulder, however, as noted above, bedrock and gravel may provide crucial attachment surfaces for ovipositing by LLFR.

One study suggests that differences in substrate permeability might affect the spatial distribution of Arizona ranid frogs, including LLFR. Specifically, Howland et al. (1997) suggest that the permeability of the substrate at a site can contribute to the permanence of surface water there, referring to sites such as cattle tanks that may be perched above the water table.

Differences in substrate stability can affect the suitability of a site for LLFR, apparently independent of the type of substrate present. Sredl et al. (1997a) and Swann and Wallace (2010) (also see Parker 2006; Wallace et al. 2010) found that large influxes of sediment (e.g., from extreme upland erosion) can extirpate LLFR or greatly reduce their abundance at pools where they were previously abundant. Sites buried by such deposition can remain buried and, therefore, unoccupied for years (Parker 2006). Conversely, flow events that scour and thereby reopen pools can have the opposite effect on LLFR occupancy (Sredl et al. 1997a). Sredl (2018) notes that sedimentation into LLFR habitat is a general risk factor in watersheds, where erosion increases due to grazing or other disturbance.

Finally, other habitat elements may affect substrate stability at locations with or potentially suitable for LLFR habitat. Non-native crayfish and some non-native fishes disturb benthic sediment, and this disturbance may reduce the suitability of these locations for leopard frogs such as LLFR in addition to the impacts of predation by these non-native species (Fernandez and Rosen 1996; Hayes and Jennings 1986). Herbaceous aquatic vegetation can stabilize substrates and slow the movement of water (Fernandez and Madsen 2013). Similarly, riparian woody and shrub vegetation can stabilize stream channel banks and allow accretion of sediment, affecting channel form and stability (Wonkka et al. 2018).

WATER CHEMISTRY

Full name: **The chemical properties of the surface water at locations with or potentially suitable for LLFR habitat within the LCR ecosystem, including the concentrations of chemical constituents and their spatial (horizontal and vertical) and temporal variation**. This habitat element addresses water chemistry parameters such as DO, pH, salinity, naturally occurring dissolved substances, and contaminants such as ammonia, nitrate/nitrite, perchlorate, selenium, mercury, other metals, artificial organic compounds and their derivatives, and organic waste products of combustion. Numerous studies document these parameters as aspects of water quality in general along the LCR, its off-channel environments, and the Bill Williams River (Arizona Department of Environmental Quality [ADEQ] 2016a, 2016b, 2016c, 2018; Hinck et al. 2007, 2009; LCR MSCP 2018a; Ohmart et al. 1988; Patiño et al. 2012; Reclamation 2004, 2010, 2011a, 2011b; Seiler et al. 2003; Stolberg 2009, 2012; Tuttle and Orsak 2002). Contaminants in the waters along the LCR and Bill Williams River valleys arrive from both point and non-point sources (see chapter 5). Water storage-delivery system design and operations (see chapter 5) also affect water

chemistry along the LCR and Bill Williams River, including salinity and DO concentrations, through their effects on reservoir operations and releases, and diversions and flow management for off-channel wetlands. Other habitat elements also affect water chemistry at any given location, particularly water depth and flow, water temperature, the amount of POM present, and their variation over time.

As noted in chapter 3 (see "Chemical Stress"), amphibians worldwide—including members of the *R. pipiens* complex—suffer deformities and altered patterns of growth, neurologic and reproductive impairment, and mortality from agricultural, industrial, and urban pollutants that cause harm either directly or following bioaccumulation (Bank et al. 2007; Blaustein et al. 2003; Brühl et al. 2013; Davidson et al. 2002; EPA 2016; Mann et al. 2009; Smalling et al. 2015; Unrine et al. 2004). The potentially harmful conditions and contaminants identified in this literature can be compared to the known water chemistry of the LCR and Bill Williams River to identify conditions and contaminants of potential concern. For example:

- As noted in chapter 2, Ruibal (1959 *in* Sredl 2018) documented a strong sensitivity to elevated water salinity in all LLFR life stages. The LCR MSCP continues to monitor water salinity in a wide range of habitats because of its potential effects on several species covered by the HCP (LCR MSCP 2016, 2018a, 2018b; Reclamation 2004).

- Selenium contamination in the LCR (Hinck et al. 2007; Reclamation 2010) is a concern because of its possible effects through bioaccumulation in bonytail, flannelmouth suckers, and razorback suckers, and in California black rails, Yuma clapper rails, and least bitterns (LCR MSCP 2018a, 2018b). Frogs also bioaccumulate selenium, which in turn impairs frog reproduction (EPA 2016). The LCR MSCP monitors selenium in backwaters in areas where LLFR habitat may occur (LCR MSCP 2018a, 2018b).

- Mercury bioaccumulation to potentially harmful levels has been detected in fishes along the LCR (Hinck et al. 2007, 2009; Tuttle and Orsak 2002) and in Alamo Lake on the Bill Williams River upstream of LLFR habitat (ADEQ 2016a, 2016b, 2018). The literature does not indicate whether mercury also occurs downstream from Alamo Lake in the Bill Williams River or its food web, particularly along the reach where LLFR are abundant (O'Donnell and Leavitt 2017a, 2017b).

- The non-native golden alga (*Prymnesium parvum*) has been detected in the LCR valley, in Beal Lake, a section of the Havasu National Wildlife Refuge adjacent to Topock Marsh (LCR MSCP 2014), and could expand to other isolated, slack-water settings. Blooms of the species produce a

toxin harmful to most fish species, although blooms occur only under special circumstances determined by water temperature and chemistry (Brooks et al. 2011; Roelke et al. 2011).

- The waters of the Bill Williams River in and downstream from Alamo Lake contain ammonia at concentrations recognized as harmful to fishes and other aquatic life (ADEQ 2016a, 2016b, 2018), including to the northern leopard frog in laboratory studies (Mann et al. 2009). Ammonia (NH_3) can cause mortality in all life stages for frogs and also cause deformities in developing embryos (Mann et al. 2009). These effects of ammonia vary with water temperature (see below, this chapter).

However, in general, the water chemistry in known and potential LLFR habitat, and the ways in which this chemistry may affect LLFR, are not topics of ongoing research among LCR MSCP work tasks (LCR MSCP 2018a, 2018b).

WATER TEMPERATURE

Full name: **The water temperature at locations with or potentially suitable for LLFR habitat within the LCR ecosystem and its horizontal, vertical, and temporal variation**. This habitat element refers to the water temperature at individual locations potentially usable, used by, or avoided by LLFR and to the ways in which water temperature varies over time and space within and between these locations. Water temperature at any single location and time may vary spatially in two dimensions: horizontally across the wetted area of each location and vertically from the water surface to the bottom of the water column. Water temperature and its variation within and between locations may affect the timing of LLFR breeding activity, growth rates, and vulnerability to thermal and chemical stress; the suitability of individual locations for LLFR in different life stages; and the suitability of these locations for species that may prey on or compete with LLFR. Water temperature and its variation within and between locations also may affect or be affected by other habitat elements such as herbaceous vegetation and aspects of the hydrologic regime. The following paragraphs discuss each of these potential causal relationships with water temperature.

The AZGFD (2006) (also see LCR MSCP 2016; Sredl 2018) notes that "[p]roximate cues that stimulate mating in *L. yavapaiensis* are not well studied, although rainfall and water temperature have been mentioned as cues for other leopard frog species in the Southwest." Rainfall seems an unlikely candidate as a cue for LLFR mating since its typical timing across the historic range of LLFR does not bear any relationship to the timing of LLFR mating (see chapter 3, "Mating and Ovipositing"). The spring LLFR mating season is not predictably rainy, and the onset of the southwestern "monsoon" rainy season coincides with

the end rather than the beginning of the LLFR mating season (Sartorius and Rosen 2000; Sredl 2018). Instead, changes in air and/or water temperature appear salient as potential cues for LLFR mating: LLFR may mate simply when water temperatures allow, particularly in geothermal springs, regardless of whether rainfall has occurred recently or not (Sartorius and Rosen 2000; Sredl 2018). LCR MSCP (2016) summarizes several studies reporting observations of winter (January) breeding in springs with warm water temperatures. The literature does not otherwise provide information on whether or how the timing of LLFR mating may vary with air or water temperature, although mating in the related northern leopard frog does appear to be primarily cued by changes in temperature (Rorabaugh 2018a).

Frost and Platz (1983) and Platz (1988) report that, as with other anuran frogs, the pulse rate and note duration of the LLFR breeding call vary with air temperature and, therefore, potentially with water temperature as well. These two features of breeding calls among anuran frogs also vary with temperature. Frost and Platz (1983) and Platz (1988) report that the *patterns of variation* of LLFR breeding call pulse rate and note duration with air temperature both differ from the patterns found in other southwestern leopard frogs. The investigators argue that these differences help maintain LLFR reproductive isolation even when other related leopard frogs occupy the same pools.

Sartorius and Rosen (2000) found that "[d]evelopment time of [LLFR] egg masses in March 1995 (n = 4) ranged from 15 to 18 days with a water temperature of 14.2 °C measured within 2 cm of the mass, 5 cm below the water surface, at 1400 h." Ruibal (1959, 1962 *in* Sredl 2018) found that LLFR eggs in a population in southern California developed fully in waters between 11 and 29 °C but also did not find LLFR egg masses in waters warmer than 25 °C. (At the time of the study, the LLFR was not recognized as a separate species but rather as the lowland form of *R. pipiens*). The literature does not otherwise provide information on whether or how LLFR egg or larval-juvenile development may vary with water temperature, although related species such as the northern leopard frog do show such variation (Rorabaugh 2018a):

- Zweifel (1968) studied embryo development in relation to water temperature for "*Rana pipiens*" from the extreme southeastern corner of Arizona near New Mexico and the international border. However, it is not clear that the specimens studied were LLFR or another leopard frog species. LLFR were recognized at that time only as a lowland variety of the northern leopard frog and were later reclassified (Platz 1988).

- Goldstein et al. (2017) report that relict frog tadpoles raised in aquaria maintained at 15, 20, 25, 30 and 35 °C experienced different rates of survival and development. *"Development was arrested in the 15 °C group, and survivorship declined to 64% after 191 days. However, 80% of the surviving larvae remained alive after the temperature was increased*

> *to 25 °C. Of these, 96% reached metamorphosis. Survivorship of the 20, 25 and 30 °C acclimation groups was 82, 94 and 66%, respectively, whereas none survived at 35 °C. Time to metamorphosis was significantly shorter for the 25 °C group (67 ± 1 days), followed by the 30 °C (98 ± 2 days) and 20 °C (264 ± 7 days) groups."*

Mann et al. (2009) summarize reports that water temperature can affect sex ratios in amphibians as follows: "Specifically, several amphibian species are masculinized by high temperatures or feminized by low temperatures during larval life and manifested as distorted sex ratios obtained at or soon after metamorphosis." However, no studies have been conducted to look for such possible effects of temperature on sex ratios among LLFR or any closely related species.

LLFR appear to tolerate a broad range of temperatures for year-round habitat. However, other than the studies of egg development by Ruibal (1959, 1962 *in* Sredl 2018), the literature on LLFR includes only anecdotes and no formal studies quantifying this range of tolerance. For example:

- Hayes and Jennings (1986) note that "[a]mong ranid frogs, high temperatures are tolerated least during early embryonic development … and breeding is probably restricted to sites and time intervals where embryos can avoid lethal temperatures."

- Howland et al. (1997) report that, for Arizona leopard frogs in general, "[t]he August 1995 reduction in counts is easily explainable. As available surface water and aquatic habitat became scarce along with increasing heat and aridity, frogs reduced activity while seeking refuge, thus becoming less detectable by our survey techniques. Increased counts in September 1995 were due to influx of water from summer rains. Decreased counts in November 1995 through March 1996 were presumably due to reduced activity with low winter temperatures." The authors also note that "… a high level of detectability could probably be increased by restricting surveys to periods favorable for frog activity as measured by such simple factors as air and water temperature, cloud cover, and wind speed."

- Sartorius and Rosen (2000) note for LLFR that "[t]adpoles that hatch in fall may share some of the benefits of spring hatchlings, including avoidance of summer drought and late summer flood scour. However, at hatching they face lower temperatures and reduced primary productivity, which prolong larval development and extend exposure to predation, fall and winter drought, and cold floods in late winter. Adult survivorship appears to be low in this species (P. Fernandez, personal observation; M. Sredl, personal communication), and we suspect that the low probability of surviving winter may contribute to the evolutionary ecology of the fall breeding period."

- Wallace et al. (2010) found LLFR along the canyons they studied at elevations of 850 to 1,460 m. "[A]verage daily air temperatures ranged from 21 °C to 38 °C during summer and from 3 °C to 20 °C during winter, and water temperatures ranged from lows of 5 °C during winter to highs of 24 °C during summer."

- Sredl (2018) summarizes multiple studies indicating that "[t]he constant flow and warm water temperature of thermal springs … permit year-round adult activity and winter breeding."

Better data are available on temperature tolerances among relict frogs. Goldstein et al. (2017) studied the temperature ranges selected by relict frog tadpoles raised in aquaria maintained at 15, 20, 25, 30, and 35 °C, respectively, when the tadpoles from each "acclimation group" were introduced into aquaria in which the water varied along a 10 °C gradient (10–20, 15–25, 20–30, 25–35 and 30–40 °C). The experiment measured the time each of 10 tadpoles spent in the cooler, middle, and warmer thirds of each gradient: "In the coolest gradient, tadpoles from all acclimation groups selected the warmer third (> 17 °C) of the gradient. In the warmer gradients, tadpoles from the 20 and 25 °C acclimation groups selected temperatures < 29 °C, while those from the 30 °C acclimation group selected temperatures < 33 °C." The study also evaluated burst speed to determine whether physiological performance was affected by developmental temperature, and found that maximal burst speed for all acclimation groups "was greater at experimental temperatures of 25 than 15 °C." No comparable experiment has been carried out with LLFR larvae.

The thermal tolerances of other species that may prey on or compete with LLFR may affect the likelihood of such interactions in a given setting. For example, Axelsson et al. (1997) found that the northern European signal crayfish (*Pacifastacus leniusculus*) consumed more amphibian eggs at higher water temperatures. Hayes and Jennings (1986) note that, in contrast to the pattern seen among native ranid frogs of the Western United States,

> *… oviposition and developmental characteristics of R. catesbeiana [*American bullfrog*] (including an embryonic CTM [*critical thermal maximum*] of 32 °C) allow it to withstand higher temperatures …. Therefore, habitat alterations that increase water temperature, such as removal of riparian vegetation or reductions in stream flow, might favor bullfrogs.*

Similarly, a more general ecological risk assessment for the American bullfrog (USFWS 2017) note that "[t]hey have a much higher critical thermal maximum than most other frogs, meaning that they are able to thrive in higher water temperature, and have a longer breeding season and a higher rate of pre-metamorphic survivorship, which also allows them to be more successful than

other frogs." However, no studies have been conducted to specifically look for interactions between LLFR and any other species that may prey on or compete with LLFR, in which water temperature may affect these interactions.

Cooler water temperatures and particularly drops in temperature appear to affect LLFR susceptibility to die-offs from red-leg and *Bd* infections (Bradley et al. 2002; Hayes and Jennings 1986; LCR MSCP 2016; Mann et al. 2009; Rosen et al. 2013; Sredl et al. 1997a; also see above, this chapter, "Infectious Agents" and chapter 3, "Disease"). LLFR living in or temporarily placed in warmer waters appear better able to fend off or recover from at least *Bd* infections (see above, this chapter, "Infectious Agents" and chapter 3, "Disease."

Finally, LLFR sensitivity to potential chemical stressors also appears to vary with water temperature. As noted in this chapter, "Water Chemistry," and chapter 3, "Chemical Stress," Sredl et al. (1997a) observed an episode during which "… a high detritus load in the pond, coupled with lowering of water level, high water temperature, and low concentrations of DO, combined to form an anoxic environment suitable for proliferation of sulphur-producing bacteria. This event reduced a population of 60–80 adult [LLFR] to fewer than 10." Mann et al. (2009) more specifically tabulate and summarize reports of agricultural chemical effects on amphibians, including the embryos and larvae of the northern leopard and the common spring peeper of eastern North America. One study summarized by Mann et al. (2009) indicated that "[i]n cold water (12 °C), both frog species were more sensitive to unionized ammonia (NH_3) than were other test-species (96 h LC_{50}s, 0.42 and 0.46 mg NH_3/L, for *R. pipiens* and *H. crucifer*, respectively). Increasing the temperature to 20 °C increased the LC_{50} to 1.9 mg NH_3/L for *R. pipiens*." Mann et al. (2009) similarly report that water temperature can affect the ways and magnitude of effects of different pesticides on different amphibians. In turn, Bank et al. (2007) summarize multiple studies indicating that "[a]cidified freshwater ecosystems with high temperatures, DOC [dissolved organic carbon], sulfate-reducing bacteria, sulfate, or inorganic Hg(II) [mercury cation] levels facilitate MeHg [methyl-mercury] bioaccumulation and biomagnification." No studies have been conducted to specifically investigate such possible interactions between water temperature and the effects of different chemical contaminants on LLFR biology.

WOODY VEGETATION

Full name: **The taxonomic composition and density of the woody vegetation assemblages at locations with or potentially suitable for LLFR habitat within the LCR ecosystem and their immediate surroundings, and spatial and temporal variation in these properties**. Woody vegetation includes both

canopy and shrub vegetation greater than 0.5 m in height, following the definitions for this CEM (see "Definitions" immediately following the acronym list).

Cotten (2011), Sredl et al. (1997a), Wallace et al. (2010), and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017) identify the woody species found at sites occupied by LLFR in southeastern and central Arizona as well as along the LCR and Bill Williams River valleys. Woody vegetation reported in and immediately surrounding LLFR habitat include Fremont cottonwood (*Populus fremontii*), Goodding's willow (*Salix gooddingii*), junipers (*Juniperus* spp.), mesquites (*Prosopis* spp.), netleaf hackberry (*Celtis reticulata*), saltcedar (non-native), seepwillow (*Baccharis glutinosa*), sugar sumac (*Rhus ovata*), velvet ash (*Fraxinus velutina*), catclaw acacia (*Acacia gregii*), buttonbush (*Cephalanthus occidentalis*), oaks (*Quercus* spp.), Arizona walnut (*Juglans major*), and Arizona sycamore (*Platanus wrightii*). The latter seven occur in association with LLRF habitat in the eastern portions of its range (Sredl et al. 1997a; Wallace et al. 2010) and may not occur along the LCR or Bill Williams River valleys.

As discussed earlier in this chapter, "Herbaceous Vegetation" and in chapter 3, "Resting/Hiding," LLFR select locations for resting and breeding with greater aquatic vegetative cover immediately overhead and greater canopy cover along the nearest shoreline compared to surrounding aquatic-wetland site conditions (Cotten and Leavitt 2014; Leavitt et al. 2017). Statistical findings confirm anecdotal records that LLFR select microhabitats for resting and breeding with emergent aquatic vegetative cover and nearby littoral canopy cover (AZGFD 2006; Sredl 2018; Swann and Wallace 2010). On the other hand, not only herbaceous vegetation, but woody vegetation, at higher densities tends to exclude LLFR from using the affected sites. AZGFD surveys of locations with or potentially suitable for LLFR habitat and their immediate surroundings, not only along the LCR and Bill Williams River valleys but also along the Agua Fria and Verde River valleys to the east, specifically examined this relationship (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017). Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016) examined the characteristic of plots at sites with LLFR compared to sites without LLFR. Leavitt et al. (2017) studied sites used by LLFR specifically for breeding to examine the relationship between intensity of use (based on counts of egg masses) and site conditions, including vegetation cover. These investigations found that LLFR avoid sites with higher densities of canopy, and use sites for breeding less, the greater the density of canopy above some optimal range. As noted above, this chapter (see "Herbaceous Vegetation)", the relict leopard frog has a similar pattern of habitat selection for resting and breeding, although it may select even more open habitat with less herbaceous or woody vegetation cover (Bradford et al. 2004, 2005; Harris 2006; Jaeger et al. 2010, 2014).

The AZGFD authors did not analyze their data to try to quantify an optimal range of canopy densities for LLFR habitat or breeding site selection. However, Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014) do note that saltcedar particularly reduces habitat quality for LLFR when this introduced woody species is present at high density.

As discussed in the LCR MSCP conceptual ecological models for other species (Braun 2018c, 2018d), the riparian vegetation of the LCR ecosystem has changed (Ohmart et al. 1988) from its historic condition as a result of river regulation, direct soil and vegetation disturbance by human activity, livestock grazing, fire control, land conversion to farming with associated irrigation and drainage, and introductions of non-native plants and animals. The introduction of saltcedar in particular has greatly altered riparian woody vegetation along both the LCR and Bill Williams River valleys.

Saltcedar is a highly invasive species that competes aggressively with native riparian vegetation throughout the Southwestern United States, including in the LCR ecosystem (Zouhar 2003). It gets its common name from its ability to tolerate saline soils very well (Zouhar 2003), but it does not require high salinity. It can out-compete most native woody and herbaceous plants wherever groundwater is sufficiently close to the ground surface to allow the invader to become established, forming large, dense monotypic stands (Merritt and Poff 2010; Meyer 2005; Nagler et al. 2011; Zouhar 2003;). A substantial amount of literature also documents that saltcedar stands in the Southwestern United States, including along the LCR valley, harbor different spectra of arthropods, birds, and herpetofauna compared to native riparian communities (Andersen and Nelson 2013; Bateman et al. 2013; Pendleton et al. 2011).

Natural resource managers throughout the Southwestern United States have fought the spread of saltcedar for decades. Restoration efforts initially involved killing and, often but not always, removing individual saltcedar trees and stands using fire, herbicides, and/or mechanical methods. Some restoration projects included planned revegetation following removal, while others simply allowed uncontrolled colonization and succession to play out (Andersen and Nelson 2013; Bateman et al. 2013; Bean and Dudley 2018; Nagler et al. 2011; Zouhar 2003). In 2001, the intentional release of the non-native northern tamarisk beetle (*Diorhabda carinulata*) in the Upper Colorado River Basin added biocontrol to the toolbox of methods (Bean and Dudley 2018). The beetle has spread widely, including down the Colorado River Valley into the LCR ecosystem, as far south as the Imperial National Wildlife Refuge as of January 2019 (RiversEdge West 2019). Repeated defoliation by the beetle usually causes the canopy to die back within 1 to 4 years, and causes plant death within 2 years or more, depending on the site (Bean and Dudley 2018).

The likely effects of saltcedar defoliation and die-back along the LCR ecosystem in the wake of northern tamarisk beetle attacks are not well understood. Die-offs

of formerly monotypic stands of saltcedar within the LCR ecosystem in or surrounding areas potentially suitable for LLFR habitat could open up habitat for native riparian vegetation. However, numerous studies suggest that, following the elimination of saltcedar, restoration of habitat quality for native plants and animals requires deliberate, controlled revegetation to avoid the emergence of undesirable plant assemblages (Bay and Sher 2008; Bean and Dudley 2018; Eckberg and Rice 2016; González et al. 2017a, 2017b; Kennard et al. 2016; Nagler et al. 2017; Nelson 2009; Nelson and Wydoski 2013; Shafroth et al. 2008; Sogge et al. 2008; Trathnigg and Phillips 2015).

Changes in the extent or density of saltcedar could affect the hydrologic regime at adjacent surface water sites through their effects on evapotranspiration from the riparian water table (Leenhouts et al. 2006; Shafroth et al. 2005; Stromberg et al. 2007, 2009). As noted in this chapter, "Herbaceous Vegetation," Reclamation prepares annual reports on evapotranspiration and evaporation along the LCR valley (Reclamation 2014, 2018). These reports consistently indicate that the annual rate (in inches) of evapotranspiration from dense stands of saltcedar (crown closure > 80%) is 44 to 50% lower than the annual rate from open water above Imperial Dam and 66 to 68% lower below Imperial Dam (Reclamation 2018). The contrast between open-water and dense saltcedar evapotranspiration along the LCR valley is less during the hottest months but follows the same pattern: The rate of evapotranspiration from areas of dense saltcedar in June is 12 to 22% lower than the open-water rate above Imperial Dam and 36% lower below Imperial Dam (Reclamation 2018). Thus, for example, removal of saltcedar from an area above Imperial Dam could increase the rate of riparian water loss, affecting the rate of pool shrinkage and streamflow decline during summer.

Changes in the extent and/or density of cottonwood-willow vegetation in riparian zones adjacent to surface water sites similarly could affect hydrologic conditions in the surface water sites, but in the opposite direction. The Reclamation reports on evapotranspiration define "cottonwood-willow" areas as areas with 61 to 100% canopy of cottonwood and willow and find that the annual rate of loss from cottonwood-willow areas exceeds that from open water by 3 to 8% north of Imperial Dam but by 18 to 19% below the dam (Reclamation 2018). The contrast follows a different pattern during June, when losses from cottonwood-willow areas above Imperial Dam exceed those from open water by 9 to 16%, but only by 1% below the dam (Reclamation 2018). Consequently, changes in the extent and/or density of cottonwood-willow vegetation could affect hydrologic conditions along the LCR valley but in different ways north versus south of Imperial Dam.

Beyond the problems created by saltcedar and its removal, woody vegetation in the LCR ecosystem potentially can affect LLFR in five ways, as cover for larvae-juveniles and adults, as food and feeding surfaces for larvae, as habitat for potential prey for adult LLFR, as habitat for potential predators of all life stages

of LLFR, and as attachment surfaces for ovipositing during LLFR breeding. Additionally, some characteristics of the woody vegetation assemblages affect the effectiveness of VES methods for monitoring LLFR and, therefore, may affect understanding of LLFR habitat preferences. The following paragraphs discuss these six types of interactions, beginning with the effects on monitoring. The discussion parallels that for herbaceous vegetation earlier in this chapter.

The investigation of the effectiveness of VES methods for monitoring Arizona ranid frogs in general by Howland et al. (1997) found that lower densities of vegetation—both herbaceous and woody—enhance the visibility of leopard frogs for VES detections, while higher densities impair it. The investigators caution that vegetation density—again, both herbaceous and woody—therefore may affect VES results. Sredl et al. (1997a) had to abandon VESs altogether at one site in their mark-recapture study because of a substantial increase in vegetation density. Similarly, AZGFD investigators consistently report that the density of woody vegetation at locations with or potentially suitable for LLFR habitat can affect monitoring along the LCR and Bill Williams River valleys (Cotten and Grandmaison 2013; Cotten and Leavitt 2014; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b). High densities of saltcedar in particular impaired the ability of field teams to visually detect LLFR or even enter areas of potential LLFR habitat.

As noted earlier in this chapter, "Herbaceous Vegetation," AZGFD teams surveying for LLFR in the LCR, Bill Williams River, Agua Fria River, and Verde River valleys sought to compensate for the effects of high densities of herbaceous and woody vegetation on the probability of detecting LLFR by the following methods (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Cotton et al. 2015, Leavitt et al. 2017; Miller and Cotten 2016; O'Donnell and Leavitt 2017a, 2017b; also see chapter 4, "Monitoring, Capture, Handling"):

- Using dip nets to attempt to capture LLFR in dense vegetation to confirm their presence (Rosen et al. 2013; Sredl et al. 1997b; Swann and Wallace 2010).

- Taking more time to conduct VES monitoring in dense vegetation, including forcing transects through the vegetation.

- Supplementing VES efforts with an audio broadcast call/response component (VES C/R), FTAs left in place for 2 nights, eDNA sampling, and nighttime DAR sampling.

Again, as noted earlier in this chapter, "Herbaceous Vegetation," O'Donnell and Leavitt (2017b) report that VESs had the highest probability of detecting LLFR presence/absence in field plots during AZGFD studies along the LCR and Bill Williams River valleys. The study did not evaluate how the different methods (VES, VES C/R, FTA, eDNA sampling, DAR) varied in their ability to

assess LLFR abundance or in their ability to detect LLFR in dense versus sparse vegetation—either herbaceous or woody. However, the investigators note that dense vegetation—again, both herbaceous and woody—may reduce the transmission of sound, affecting the results of VES C/R and DAR monitoring, and that FTAs were particularly effective in detecting LLFR in dense vegetation.

Woody vegetation in the LCR ecosystem, and litter produced by this vegetation, can provide cover habitat for LLFR larvae-juveniles and adults. The AZGFD (2006) summarizes several reports on LLFR habitat use as follows: "Shallow water with emergent and perimeter vegetation provides basking habitat and deep water, root masses, undercut banks, and debris piles provide refuge from predators and potential hibernacula." The root masses and debris may be parts of or derive from woody vegetation. For example, Sredl et al. (1997a) selected the six sites for their LLFR mark-recapture study in part because their low densities of woody shoreline vegetation made them particularly suitable as LLFR habitat.

Female LLFR specifically select sites for ovipositing based in part on the density of canopy available. The detailed study by the AZGFD of LLFR breeding site selection patterns along the Bill Williams, Agua Fria, and Verde River valleys (Leavitt et al. (2017) found that "… the majority of sites selected … for oviposition had [a] higher canopy than the randomly selected sites and were relatively close to [canopy] cover and sites where they could crawl out of the water." The study found that LLFR oviposited under the following canopy types (numbers indicate counts of occurrences out of a total of 62 observed egg masses): "None (33); unknown (15); willow (12); cottonwood (1); tamarisk (1)." Ovipositing occurred under an average of 15.63 ± 3.11% canopy cover.

The canopy provided by woody vegetation may also shield LLFR adults in particular from exposure to high levels of UV-B radiation. As noted in chapter 3, "Chemical Stress," UV-B radiation can kill amphibians directly, cause sublethal effects, or exacerbate the effects of other sources of stress (Blaustein et al. 2003). However, investigators have not studied the effects of UV-B on LLFR.

As noted in chapter 2 and chapter 3, "Foraging," the diet of LLFR larvae likely includes organic debris, and algae (*aka* periphyton or aufwuchs) growing on the surfaces of submerged plant tissues. Litter from woody vegetation presumably may serve as one of the sources of this organic debris and as surfaces on which periphyton may grow and, therefore, on which LLFR larvae may forage.

LLFR adults feed within the stands of woody vegetation that they also use for canopy cover, except during inter-site movement (see chapter 3). The composition and density of the woody vegetation in and immediately surrounding sites occupied by LLFR presumably affects the types and abundance of the arthropods and other invertebrates on which LLFR adults feed, including beetles, flies, terrestrial stages of aquatic invertebrates, spiders, earthworms, slugs, and snails (see chapter 3, "Foraging"). However, no studies address how the

composition and density of the woody vegetation in and immediately surrounding sites occupied by LLFR may affect LLFR adult foraging options or behaviors.

The composition and density of the woody vegetation in and immediately surrounding sites occupied by LLFR also affects the types and abundance of species that may prey on LLFR eggs, larvae-juveniles, or adults. As noted above, this chapter (see "Birds and Mammals," "Fish and Herpetofauna," and "Macroinvertebrates") and chapter 3 (see "Predation"), the list of potential predators of LLFR along the LCR and Bill Williams River valleys necessarily consists of species that may live in or at least visit LLFR habitat. However, the literature on LLFR does not systematically address how the composition and density of the woody vegetation in or surrounding sites occupied by LLFR may affect the composition, abundance, or foraging behaviors of the many species of birds, mammals, fishes, herpetofauna, or macroinvertebrates that may prey on LLFR at these sites.

As discussed in this chapter, "Herbaceous Vegetation" and chapter 3, "Ovipositing," LLFR females use submerged vegetation as attachment surfaces during ovipositing. The detailed study by the AZGFD of LLFR breeding site selection patterns along the Bill Williams, Agua Fria, and Verde River valleys (Leavitt et al. [2017]) found that the plants on which LLFR oviposited included submerged sections of saltcedar, willow, cottonwood, and leaves and twigs for which taxonomic identification in the field was not possible.

Finally, woody vegetation may affect LLFR indirectly, for example, by affecting the fire regime (fuel loads), periphyton (as surfaces on which periphyton can grow) and POM in the water, and hydrology at locations with or potentially suitable for LLFR habitat, as discussed elsewhere in this chapter).

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics, both natural and anthropogenic, that affect the abundance, spatial and temporal distributions, and quality of habitat elements. Controlling factors may also significantly directly affect some critical biological activities or processes. A hierarchy of controlling factors exists, with long-term dynamics of climate and geology at the top; however, this CEM focuses on 10 immediate controlling factors that are within the scope of potential human manipulation, particularly manipulation by the LCR MSCP and its conservation partners.

The 10 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.

Table 6 lists the 10 controlling factors included in the LLFR conceptual ecological model and the habitat elements they directly affect. Controlling factors affect habitat elements indirectly, as well, through their effects on other controlling factors or through the cascading effects of habitat elements on each other.

CHANNEL AND OFF-CHANNEL ENGINEERING

Full Name: **The engineering activities of Reclamation, the USFWS, and the States and Tribes focused on managing the geomorphology of the LCR channel and off-channel habitats, including in conservation areas and wildlife refuges**. This factor covers both historic and ongoing activities such as dredging, shoreline armoring, construction and maintenance of river levees and training structures, construction and maintenance of connected backwater environments and non-connected ponds, and other modifications in areas of development or habitat management (Reclamation 2004; LCR MSCP 2018a). These activities strongly shape the depth profiles, shorelines, and substrates of the targeted and adjacent locations as well as sediment dynamics throughout the system. Reclamation carries out relatively little mechanical shaping along channel and off-channel habitats, but both Reclamation and other agencies, such as the USFWS, have ongoing engineering programs to maintain, reshape, and create habitat in non-connected ponds (LCR MSCP 2018a).

Table 6.—LLFR controlling factors and the habitat elements they are proposed to directly affect among the three LLFR life stages (Xs indicate which controlling factors may affect each habitat element.)

Habitat element ➔ / **Controlling factor 🡻**	Airborne contaminants	Birds and mammals	Drainage network connectivity	Fire regime	Fish and herpetofauna	Herbaceous vegetation	Hydrologic regime	Infectious agents	Macroinvertebrates	Monitoring, capture, handling	Periphyton and particulate organic matter (POM)	Substrate	Water chemistry	Water temperature	Woody vegetation
Channel and off-channel engineering							X					X			
Conservation monitoring and research programs					X					X					
Fire management				X											
Fisheries management					X										
Land use	X	X			X	X	X		X						X
Nuisance species introduction and management		X			X	X		X	X		X				X
Onsite vegetation management	X			X		X									X
Onsite water management			X	X			X						X	X	
Wastewater and other contaminant inflows								X					X		
Water storage-delivery system design and operations			X				X					X	X	X	

CONSERVATION MONITORING AND RESEARCH PROGRAMS

Full Name: **The types, frequencies, and duration of monitoring and research activities carried out by the LCR MSCP, USFWS, States, and Tribes focused on species and habitats of concern to their respective wildlife conservation programs**. The HCP mandates the LCR MSCP, in particular, to carry out conservation measures to meet the biological needs of 5 threatened or endangered species and 19 other covered species, and potentially benefit 5 evaluation species. The HCP identifies the LLFR as an evaluation species (Reclamation 2004). 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 LLFR (LCR MSCP 2018a, 2018b).

FIRE MANAGEMENT

Full name: **The types, frequencies, and duration of activities intended to control and/or suppress fire at locations with or potentially suitable for LLFR habitat within the LCR ecosystem as well as 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 (Reclamation 2018). Wildfire is a natural type of disturbance in the riparian plant communities of the LCR valley, and wildfires today also occur through human accidents (Conway et al. 2010; LCR MSCP 2018a; MacNally et al. 2004; Meyer 2005). In fact, wildfires have occurred recently at LCR MSCP restoration sites (Hunters Hole and Yuma East Wetlands) and in riparian habitat at the Havasu National Wildlife Refuge and Cibola National Wildlife Refuge-Island Unit (J. Hill, and C. Ronning 2018, joint personal communication; LCR MSCP 2018a, 2018b).

FISHERIES MANAGEMENT

Full Name: **The types, frequencies, and duration of activities carried out by the LCR MSCP, USFWS, States, and Tribes to manage native fish species and introduced recreational fisheries along the LCR channel and off-channel**

habitats, including in conservation areas and wildlife refuges, and the legacies of past and unofficial introductions. The LCR MSCP has lead responsibility for the management of native fish species in the LCR ecosystem under the HCP (Reclamation 2004). In turn, the States bordering the LCR recognize and oversee the sport fisheries along the LCR, its reservoirs and connected backwaters, and its tributaries. The fishes recognized by these States as sport fishes include intentionally introduced and/or stocked species and accidental introductions. The States and recreational fishers have also introduced bait and forage species to support the sport fisheries. These bait and forage species may be caught as sport fishes and may also be considered (by the States) to be nuisance species. Arizona lists the official sport fishes for the State (https://www.azgfd.com/fishing/species/) and State records for any caught along the LCR (https://www.azgfd.com/Fishing/records/). Recreational fishers also may transplant desired sport fishes to water bodies where management agencies have tried to keep them out (LCR MSCP 2017; Wolff et al. 2012).

Habitat created or managed to conserve native fishes in the Southwestern United States also potentially can contain aquatic and wetland habitat for LLFR and other native amphibians in their shallows and around their wet perimeters (Rosen and Schwalbe 1998). The present CEM (see chapter 6) explicitly recognizes that fisheries management practices affect three other controlling factors—channel and off-channel engineering, nuisance species introductions and management, and onsite water management—that in turn may affect many habitat elements that affect LLFR in one or more life stages. The present CEM also recognizes that fisheries management practices directly affect fish assemblages both on- and off-channel across the greater LCR ecosystem.

LAND USE

Full name: **The types, frequencies, and duration of major land-use activities taking place on lands that surround locations with or potentially suitable for LLFR habitat within the LCR ecosystem**. The major land-use activities of concern for this factor include wildlife conservation, irrigation farming, rangeland grazing, recreation, and industrial, commercial, and residential activities associated with developed areas (Reclamation 2004). Major landowners along the LCR and Bill Williams River valleys in Arizona include the Bureau of Land Management; the State of Arizona; the USFWS; Reclamation; the Chemehuevi, Cocopah, Mohave, and Quechan Indian Tribes; and private individuals.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

Full name: **The introduction and management of nuisance species that potentially may interact with LLFR in the waters and wetlands of the LCR and Bill Williams River valleys**. Nuisance species are non-native animals, plants, and microorganisms that were not introduced and/or are not managed for recreational purposes; and may poison, infect, prey on, compete with, or present alternative food resources for native species; cause other alterations to the aquatic or riparian food web that affect native species; or affect habitat features such as vegetation cover or water chemistry. The factor includes the legacy of past introductions, and the potential for additional introductions, and includes both intentional and accidental introductions. 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 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.

Nuisance species of potential concern for the conservation of LLFR along the LCR and Bill Williams River valleys include saltcedar (see chapter 4, "Woody Vegetation"), common reed, giant salvinia (see chapter 4, "Herbaceous Vegetation"), golden alga (see chapter 4, "Water Chemistry), American bullfrog and numerous predatory non-native fishes (see chapter 4, "Fish and Herpetofauna"), northern crayfish and red swamp crayfish (see chapter 4, "Macroinvertebrates"), and *Bd*, the fungus responsible for chytridiomycosis; see chapter 4, "Infectious Agents").

ONSITE VEGETATION MANAGEMENT

Full name: **The types, frequencies, and durations of actions taken to manage the taxonomic composition, abundance, condition, and spatial distribution of vegetation at locations with or potentially suitable for LLFR habitat within the LCR ecosystem**. This factor addresses vegetation management at the scale of individual sites managed to achieve specific habitat or hydrologic goals. The LCR MSCP and other land managers along the LCR and Bill Williams River valleys use a range of methods to manage vegetation on lands under their authorities, including prescribed fire, surface irrigation and subirrigation, planting, fertilizing, thinning and hand removal, discing and plowing, and the application of herbicides (LCR MSCP 2014, 2018a). Agencies and irrigation and drainage districts may also remove vegetation to maintain roads and canals under their authorities.

ONSITE WATER MANAGEMENT

Full name: **The types, frequencies, and durations of actions taken to manage the delivery and distribution of regulated water to locations with or potentially suitable for LLFR habitat within the LCR ecosystem**. This factor addresses water management at the scale of individual sites intentionally supplied by surface water diversions and/or groundwater withdrawals, or passively supplied by seepage from adjacent surface water diversions. As noted above, LLFR can occupy manmade systems, including earthen cattle tanks, livestock drinkers, canals, and irrigation sloughs. The LCR MSCP and USFWS irrigate portions of several conservation areas along the LCR valley to create and manage habitat for general wildlife, LCR MSCP covered species, and associated wetland habitat (Cotten and Leavitt 2014; LCR MSCP 2018a). In addition, given the flexibility that LLFR exhibit in their selection of habitat, the numerous agricultural irrigation and drainage districts along the LCR valley unintentionally could create additional potential LLFR habitat along their surface waterways. Once established at a location with a hydrologic regime determined by onsite water management, LLFR will likely depend on that management to maintain suitable hydrologic conditions for their continuing presence at the site.

WASTEWATER AND OTHER CONTAMINANT INFLOWS

Full name: **The types, frequencies, and durations of wastewater and other potentially chemically altered inflows to the LCR or its tributaries, and the types, frequencies, and durations of actions taken to manage the contributions these inflows make the chemistry of the receiving waters**. The LCR receives inputs directly from large and small municipal wastewater systems. The largest of these inputs comes from Las Vegas via the Las Vegas Wash, which flows into Lake Mead. The Clark County (Nevada) Water Reclamation District, Laughlin Wastewater Reclamation Facility, discharges into Reach 3 between Davis Dam and Lake Havasu. Bullhead City, Arizona, and both Needles and Blythe, California, also operate municipal wastewater facilities, the discharges of which affect the river after passing through infiltration ponds. The Colorado River Sewage System Joint Venture, which serves Parker, Arizona, and the Colorado River Indian Reservation, discharges into an irrigation return canal that flows directly into the Colorado River. The river also receives storm runoff from all developed areas along its course and reservoirs; Lake Havasu also receives diffuse wastewater input from the septic systems of Lake Havasu City, Arizona. The lower Bill Williams River receives surface water from Alamo Lake, which the State of Arizona recognizes as a polluted water body (see chapter 4, "Water Chemistry"). Finally, non-point source pollution from irrigation return flows and storm runoff from individual sites of chemical contamination bring additional

contaminants into the LCR from Reach 3 below Davis Dam downstream (Acharya and Adhikari 2010a, 2010b; Adhikari et al. 2011; Hamilton et al. 2005a, 2005b; Reclamation 2010, 2011b; Sanchez et al. 2005; Seiler et al. 2003; Stolberg 2009, 2012).

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATIONS

Full name: **The types, frequencies, and durations of coordinated basin-scale activities that regulate the elevation of surface water along the LCR main stem**. The Colorado River through the LCR 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. 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 elevations and groundwater elevations along the main stem LCR and its floodplain (Reclamation 2004). The dams along and above the LCR also trap essentially all of the sediment and both coarse and fine organic matter that would have flowed past their locations prior to their construction. River regulation and entrenchment of the river along flowing reaches 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 valley. Reclamation, the USFWS, and other agencies have rights to use some of the water in the LCR on lands managed as wildlife habitat (LCR MSCP 2014, 2018a). Surface water elevations also may support shallow marsh habitat along shorelines and in nearby off-channel wetlands.

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains three sections, each presenting the CEM for a single LLFR life stage. For each life stage, the text and diagrams identify its life-stage outcomes; its critical biological activities and processes; the habitat elements that support or limit the success of its critical biological activities and processes; the controlling factors that determine the abundance, distribution, and other important qualities of these habitat elements; and the causal links among them.

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

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

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

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

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

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

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

The present report 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 with the present report 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.

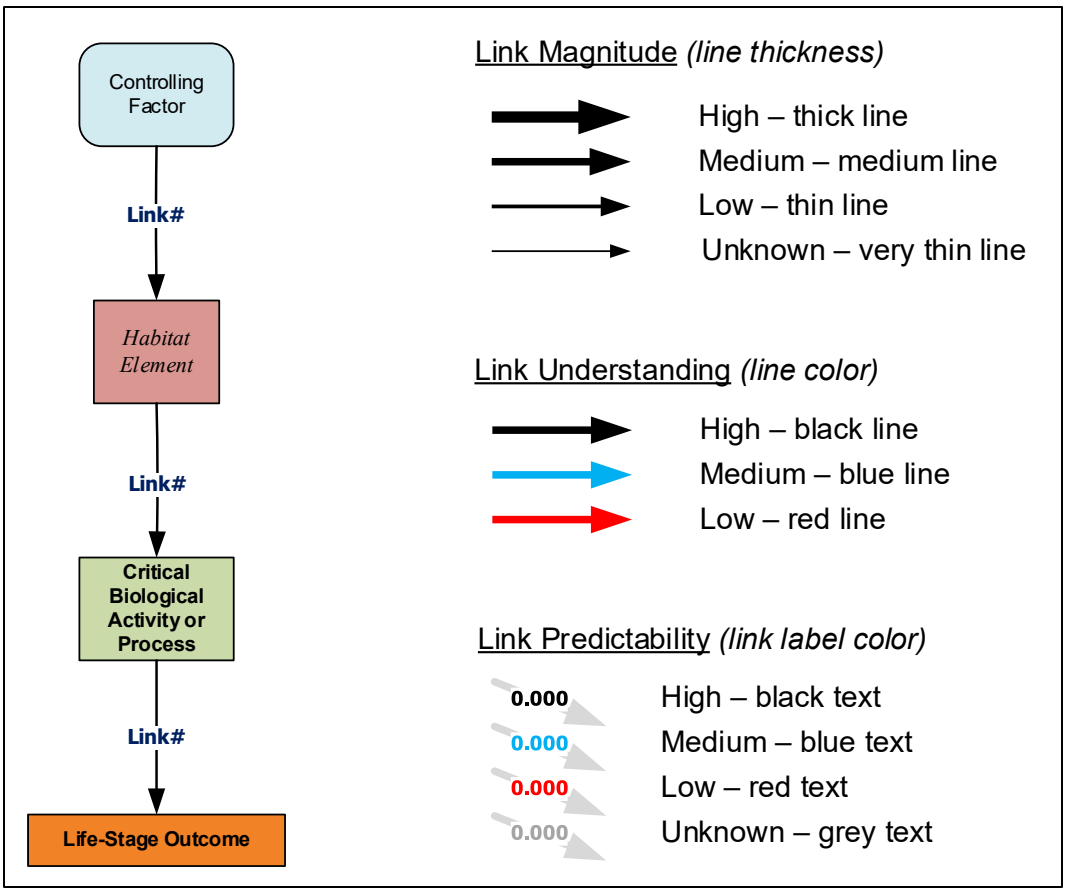

Figure 2.—Diagram conventions for LCR MSCP species CEMs.

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, and 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. Finally, the color of the label represents link predictability.

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

LLFR LIFE STAGE 1 – EGGS

As described in chapter 2, this life stage begins when LLFR adult females deposit their eggs in a water body (e.g., pond, stream pool, marsh, etc.) while they are fertilized by an accompanying male. The adults then leave the mass of fertilized eggs (clutch) to survive on their own. The life stage ends when the embryos emerge from their natal egg mass as larvae, also known colloquially as tadpoles or pollywogs. Only one study has been conducted to examine LLFR egg incubation times: Sartorius and Rosen (2000) found that LLFR egg maturation to hatching required 15–18 days in the wild. This life stage has two life-stage outcomes (see figure 1): egg growth and egg survival. 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.

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

As shown on figure 3, the CEM identifies six critical biological activities or processes affecting one or both outcomes for this life stage. However, the CEM identifies only one of these six critical biological activities or processes—predation—with a high-magnitude direct effect on either outcome – in this case, only affecting egg survival. Thus, the CEM proposes that predation has a greater effect on egg survival than does any other critical biological activity or process.

Predation is the most commonly proposed cause of mortality among LLFR in all life stages, thought to contribute significantly (along with habitat loss) to LLFR extirpation across large areas of its historic range. The literature does not address how predation rates differ specifically among the three LLFR life stages; however, among amphibians in general, eggs and larvae experience far greater rates of mortality, particularly from predation, than do adults (Duellman and Trueb 1986). LLFR preferentially breed (and eggs therefore are concentrated) in shallower, low-velocity settings with relatively low densities—but not absence—of herbaceous aquatic and riparian vegetation with partial woody canopy. Such settings are less favored by many of the non-native predators that may prey on LLFR eggs, which prefer deeper water and/or denser emergent aquatic vegetation. The AZGFD proposes that these aspects of LLFR habitat selection partially explain LLFR distribution along the Bill Williams River Valley; however, it is not clear how much of this LLFR distribution results from LLFR habitat selection that reduces their interaction with these predators versus how much is due to more intense removal of LLFR by predators in some settings versus others. More generally, no studies specifically examine predation on the eggs of LLFR or any closely related species; as a result, link understanding is rated as low.

The five other critical biological activities or processes proposed to affect either egg growth or egg survival are chemical stress, disease, hydration stress, mechanical stress, and thermal stress,. The CEM proposes that all five have low-magnitude effects on egg survival, all with low understanding due to a lack of studies of these possible effects to LLFR or any closely related species (see figure 3). The CEM also proposes that thermal stress and mechanical stress may have low-magnitude effects on egg growth; and that disease, chemical stress, and hydration stress have unknown-magnitude effects on egg growth. The CEM proposes that all these effects on egg growth again have low understanding due to a lack of studies of these possible effects in LLFR or any closely related species (see figure 3).

The CEM proposes that several of the critical biological activities and processes affect each other, possibly compounding their effects on egg growth or survival. Specifically, chemical stress and disease are proposed to affect each other, disease and hydration stress are proposed to affect each other, and predation is proposed to affect mechanical stress, all with unknown magnitude; disease and thermal stress are proposed to affect each other with low magnitude. All these interactions among critical biological activities and processes are rated as having low understanding due to the absence of reported information on these topics for LLFR or any closely related species.

The CEM identifies three habitat elements with a high-magnitude direct effect on predation on LLFR eggs: the bird and mammal, fish and herpetofauna, and macroinvertebrate assemblages. As noted above, no investigations have specifically studied predation on LLFR in any life stage; however, the literature on anurans in general indicates that birds; small mammals; aquatic

macroinvertebrates, including insect larvae and crayfish; small fishes; carnivorous larvae of other amphibians such as the American bullfrog; and reptiles such as turtles all commonly prey on anuran eggs (see chapter 3, "Predation" and chapter 4, "Birds and Mammals," "Fish and Herpetofauna," and "Macroinvertebrates"). As a result of this consistent pattern, the CEM rates the magnitude of effect of the three species assemblages on the rate of predation on LLFR eggs as high rather than unknown. At the same time, the CEM rates the understanding of these effects as low due to the absence of reported information on these topics for LLFR or any closely related species.

The CEM identifies one habitat element—infectious agents—with a high-magnitude effect on disease in LLFR eggs; two habitat elements affecting chemical stress in LLFR eggs, water chemistry with medium magnitude and airborne contaminants with low magnitude; two habitats affecting thermal stress in LLFR eggs, water temperature with low magnitude and the fire regime with unknown magnitude; three habitat elements affecting mechanical stress in LLFR eggs, substrate dynamics with low magnitude, the hydrologic regime with medium magnitude, and monitoring with unknown magnitude; and two habitat elements affecting hydration stress in LLFR eggs, the hydrologic regime with medium magnitude and monitoring with unknown magnitude. Again, the CEM rates the understanding of these effects as low due to the absence of reported information on these topics for LLFR or any closely related species.

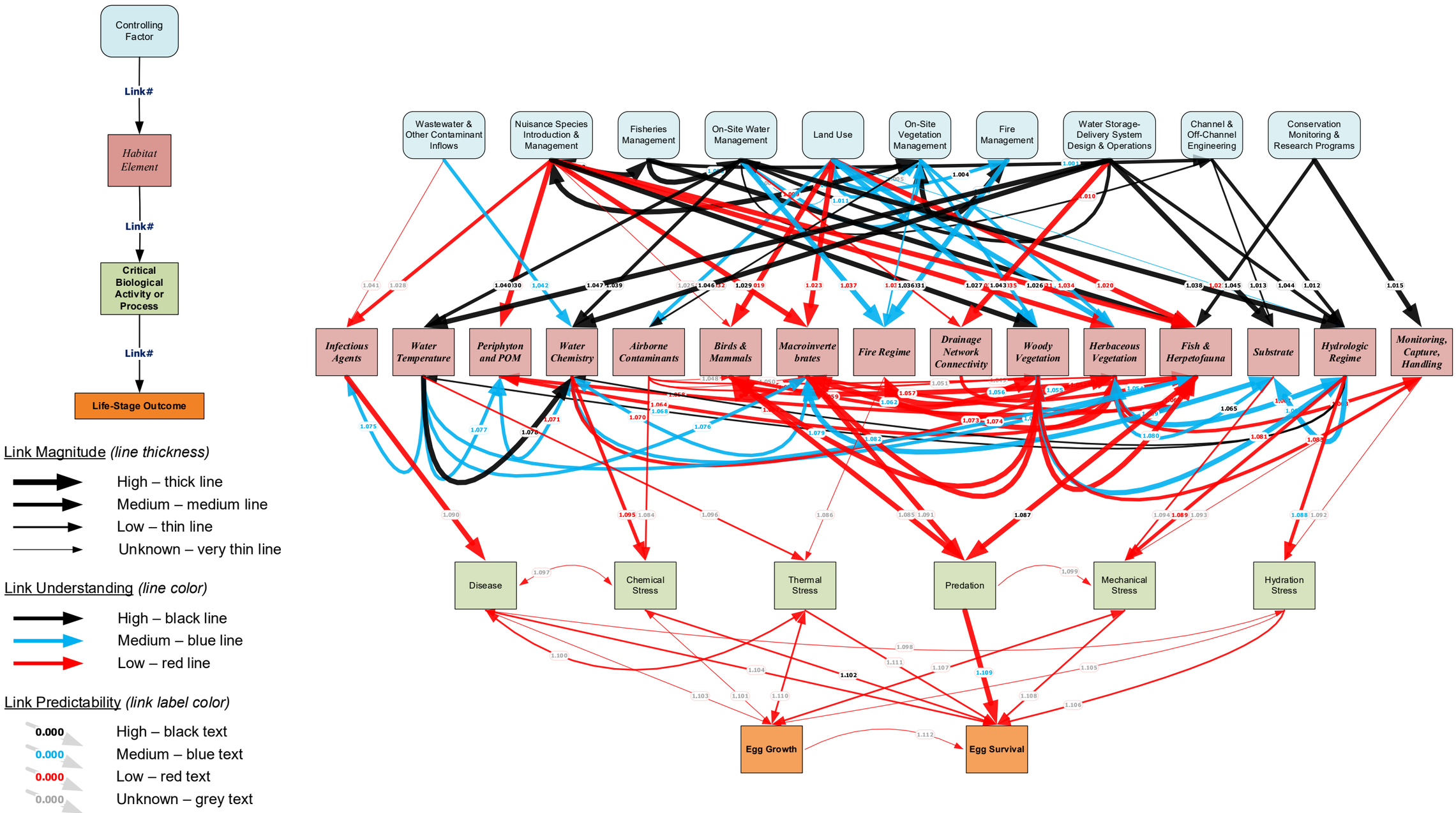

Figure 3.—CEM master diagram for LLFR life stage 1 – eggs life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LLFR LIFE STAGE 2 – LARVAE AND JUVENILES

As described in chapter 2, this life stage begins when the eggs hatch and swim away from the remains of their natal egg mass as tadpoles with eyes, a tail, and external gills. As do all frog species, LLFR then undergo several types of transformations during their brief larval-juvenile stage, culminating in a final metamorphosis into adults. Platz (1988) reports that LLFR larvae at the start of this final metamorphosis have an average length of 25–29 mm. Rorabaugh (2018b) states that LLFR larvae grow 75–90 mm "… prior to metamorphosis." This life stage ends with the completion of metamorphosis (i.e., when the frogs fully attain their adult body form and physiology). This life stage has two life-stage outcomes (see figure 1): larval-juvenile growth and larval-juvenile survival. 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.

Similar to the CEM for the egg stage, the CEM for this life stage proposes that larval-juvenile growth affects larval-juvenile survival, but with unknown magnitude. The literature for anurans in general indicates that faster larval maturation should convey lower vulnerability to a range of threats and, therefore, result in a higher rate of survival. The relationship should be strong, based on core biological principles and observations of other anurans; however, no studies have addressed the topic specifically for LLFR or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is rated as low.

The CEM identifies eight critical activities or processes that directly affect larval-juvenile survival; however, only three of these appear to have significant effects on this life-stage outcome: predation and foraging are proposed to have high-magnitude effects, and disease is proposed to have a medium-magnitude effect. Among the other five critical activities or processes, four—chemical stress, hydration stress, mechanical stress, and thermal stress—are proposed to have low-magnitude effects on survival, and one, resting/hiding, is proposed to have an unknown magnitude of effect on survival. The CEM proposes that all these effects of critical activities or processes on larval-juvenile survival have low understanding due to a lack of studies of these possible effects in LLFR or any closely related species (figure 4).

Predation, particularly by non-native fishes, amphibians, and crayfish, is the most commonly proposed cause of mortality among LLFR in all life stages, thought to contribute significantly (along with habitat loss) to LLFR extirpation across large areas of its historic range. As also noted above in this chapter, among amphibians in general, eggs and larvae experience far greater rates of mortality, particularly from predation, than do adults (Duellman and Trueb 1986). LLFR preferentially breed (and larvae and juveniles therefore are concentrated) in

shallower, low-velocity settings with relatively low densities—but not absence—of herbaceous aquatic and riparian vegetation with partial woody canopy (see chapter 4). Such settings are less favored by many of the non-native predators of concern, which prefer deeper water and/or denser emergent aquatic vegetation. The AZGFD proposes that these aspects of LLFR habitat selection partially explain LLFR distribution along the Bill Williams River Valley (see chapters 3 and 4); however, it is not clear how much of this LLFR distribution results from LLFR habitat selection that reduces their interaction with these predators and how much is due to more intense removal of LLFR by predators in some settings versus others. As discussed below, LLFR larvae and juveniles also likely have a repertoire of behaviors for avoiding predators.

The literature on anurans in general provides a wide range of examples of the impacts of predation and the impacts of predator avoidance behaviors. In turn, the literature on LLFR emphasizes the overall importance of predation as a crucial factor in LLFR population dynamics rangewide, but it does not present formal evidence of predator-survival dynamics or predator-avoidance behaviors specifically for LLFR larvae and juveniles. The literature notes that knowledge of predation on LLFR is weak and one of the major gaps in understanding the species and its conservation needs. Consequently, the causal link between predation and LLFR larval-juvenile survival is rated as having low understanding.

The CEM also proposed that LLFR foraging has a high-magnitude effect on survival in this life stage simply because foraging success is necessary for survival in all animals. Unfortunately, the literature provides extremely little information on LLFR larval-juvenile foraging, including food item selection, and no information on variability in foraging success. The literature emphasizes this gap in knowledge as a crucial area for investigation, and the CEM rates the understanding of this causal relationship as low. At the same time, the greater LCR ecosystem—and particularly its riparian and wetland habitats—is home to a wide range of the general types of small invertebrates on which LLFR larvae and juveniles are reported to feed. Further, field studies such as those by the AZGFD along the Bill Williams, Big Sandy, Agua Fria, and Verde Rivers (see chapters 3 and 4) indicate that, when present at all, LLFR always occur abundantly. These pieces of information suggest that LLFR larvae and juveniles do not suffer from foraging deficits in their preferred habitat settings.

The CEM recognizes disease as a medium-magnitude contributor to LLFR larval-juvenile mortality, primarily because based on reports of contributions of red-leg and *Bd* to LLFR mortality. Both diseases are common among Western United States ranid frogs, as discussed above (see chapter 3). The literature reports several instances of LLFR mortality up to complete extirpation of a local population as a result of these diseases; however, the literature does not indicate whether mortality in these cases varied between larval-juvenile versus adult life stages (and does not address egg mortality from disease at all). Such lethal outbreaks are associated with significant cold-weather events, in which the colder

temperatures are beneficial to the pathogens and, perhaps, also reduce resistance among the LLFR in the affected pools. Such cold-weather events are infrequent along the LCR valley, which lies in the warmer (westernmost, lowest elevation) portion of the historic range of the species, suggesting the medium-magnitude rating for its effect along the LCR. However, no studies specifically address this relationship for LLFR in the greater LCR ecosystem, prompting a low rating for understanding.

The CEM identifies seven critical activities or processes that directly affect larval-juvenile growth; however, only one of these appears to have significant effects on this life stage: foraging is proposed to have high-magnitude effect. Foraging success is a commonly recognized cause of healthy body condition and promoter of growth in all animals. The CEM proposes that this link is bi-directional: Healthier and/or larger individuals are likely to have greater foraging success. However, as noted above, the literature provides extremely little information on LLFR larval-juvenile foraging, including food item selection, and no information on variability in foraging success. The literature emphasizes this gap in knowledge as a crucial area for investigation, and the CEM consequently rates the understanding of this causal relationship as low. The greater LCR ecosystem presumably supports a suitable complement of periphyton and POM, on which LLFR larvae and juveniles are reported to feed (see chapters 3 and 4). Further, field studies such as those by the AZGFD along the Bill Williams, Big Sandy, Agua Fria, and Verde Rivers (see chapters 3 and 4) indicate that, when present at all, LLFR always occur abundantly. These pieces of information suggest that LLFR larvae and juveniles do not suffer from foraging deficits in their preferred habitat settings.

The CEM proposes that three other critical activities or processes—disease, mechanical stress, and thermal stress—have low-magnitude effects on larval-juvenile growth; and three others—chemical stress, hydration stress, and resting/hiding—have effects of unknown magnitude. The CEM again proposes that all these effects of critical activities or processes on larval-juvenile growth have low understanding due to a lack of studies of these possible effects in LLFR or any closely related species (figure 4).

The CEM proposes that several of the critical biological activities and processes affect each other, possibly compounding their effects on larval-juvenile growth or survival. Most importantly, LLFR larval-juvenile resting/hiding behaviors are proposed to affect the rate of predation with high magnitude. As with all frogs, LLFR larvae-juveniles should be able to reduce their vulnerability to predation by fleeing or engaging in behaviors to avoid detection by predators, including hiding in/under suitable cover habitat. Such behaviors are ubiquitous among frogs, and this warrants rating the proposed link as high-magnitude even though the literature provides no information on avoidance behaviors among LLFR larvae or juveniles in the presence of any predator. At the same time, however, the CEM necessarily rates understanding of the proposed link as low.

Other causal relationships among critical biological activities and processes with at least medium magnitude include a medium-magnitude, bi-directional cause-effect relationship between disease and chemical stress, and a medium-magnitude, uni-directional effect of competition on foraging. The CEM includes the relationship between disease and chemical stress because several studies of frog sensitivity to pollutants note that exposure can increase their sensitivity to disease as well; however, this has not been studied specifically for LLFR or any closely related species.

The CEM includes the relationship between competition and foraging because the abundance and range of species competing with LLFR larvae and juveniles for food should constrain LLFR larval-juvenile prey selection and foraging success. Potential competitors with LLFR larvae and juveniles for food are abundant and ubiquitous in the LCR ecosystem; however, many of these competitors are native species among which LLFR has evolved and, therefore, likely has adaptations to reduce the magnitude of the effect, such as through resource partitioning. On the other hand, some non-native competitors with LLFR larvae and juveniles may pose bigger challenges because LLFR adaptations to competition may not be as effective against non-native competitors. The subject has not been studied for LLFR or any closely related species in the region, although reports identify competition from the Rio Grande leopard frog as a possible example.

The CEM identifies three habitat elements with a high-magnitude direct effect on predation on LLFR larvae-juveniles: the bird and mammal, fish and herpetofauna, and macroinvertebrate assemblages. More information is available on predation on LLFR larvae-juveniles than on LLFR eggs. The literature on anurans in general indicates that wading birds, small mammals, aquatic macroinvertebrates, including insect larvae and crayfish; small and medium-sized fishes; carnivorous amphibians such as the American bullfrog and its larvae; and reptiles such as turtles all commonly prey on anuran eggs (see chapter 3, "Predation" and chapter 4, "Birds and Mammals," "Fish and Herpetofauna," and "Macroinvertebrates"). Evidence for predation specifically on LLFR larvae or juveniles by various birds, mammals, and macroinvertebrates (particularly crayfish) comes from general observations of the foraging behaviors of members of these taxa in the greater LCR ecosystem. For example, several wading birds that occur along the LCR valley are known to eat frogs (see chapters 3 and 4).

The evidence for predation on LLFR by particular birds and herpetofauna is more direct: The literature documents that, among fishes, the native Gila chub (*Gila intermedia*), and the non-native black bullhead, bluegill, channel catfish, flathead catfish, green sunfish and other sunfish, largemouth bass, and redbelly tilapia all definitely consume LLFR larvae, as do the American bullfrog and its tadpoles. Gila chub do not occur in the greater LCR ecosystem, but all others in this list do; however, these predators may not always occur in locations inhabited by LLFR, and vice versa, as indicated by AZGFD surveys along the Bill Williams River Valley. As a result, predation on LLFR larvae and juveniles by members of the

fish and herpetofaunal assemblage is extremely likely to occur at a high rate, and to take place throughout the year in all locations, but also is likely constrained by the effects of other habitat elements on LLFR and fish and herpetofaunal spatial activity and spatial distribution. It should also be noted that the literature suggests the possibility that LLFR adults may cannibalize LLFR larvae. The CEM assigns a rating of low for understanding for the effects of birds, mammals, and macroinvertebrates as predators of LLFR larvae and juveniles but assigns a rating of medium for understanding of the predatory effects of fish and herpetofauna on this life stage.

The CEM identifies other habitat elements with high-magnitude direct effects on other critical biological activities and processes for this life stage, as follows:

- The CEM identifies infectious agents as having high-magnitude effects on disease. The reasoning here is the same as for the egg life stage, but with greater documentation in the literature specifically for LLFR, resulting in a medium rating for understanding.

- The CEM proposes that the periphyton and POM assemblage has a high-magnitude effect on LLFR larval foraging since LLFR larvae are reported to feed primarily on these types of biomass. However, the data of LLFR larval foraging and food selection are sparse, resulting in a low rating for link understanding.

- The CEM proposes that the composition and density of the macroinvertebrate assemblage have a high-magnitude effect on competition for LLFR in this life stage. Many aquatic macroinvertebrates in the ecoregion, including insect larvae, also forage on periphyton and POM; however, no investigations have explicitly addressed the latter subject for LLFR, resulting in a low rating for link understanding.

- The CEM proposes that the densities of woody and herbaceous—particularly herbaceous aquatic—vegetation have high-magnitude effects on LLFR larval-juvenile resting/hiding success. LLFR adult breeding and ovipositing behaviors determine the composition and density of aquatic herbaceous vegetation and overhanging woody vegetation that larvae experience. Consequently, it is not technically appropriate to speak about LLFR larval or juvenile "habitat selection" with respect to their resting/hiding in herbaceous vegetation or beneath woody vegetation. However, a well-documented pattern of strong adult selection for both resting/hiding and ovipositing habitat based on herbaceous and woody vegetation conditions (see below) suggests a strong relationship affecting the larvae and juveniles as well. Further, submerged litter from woody and herbaceous vegetation likely forms an important part of LLFR larval and juvenile habitat, as the larvae and juveniles can hide within it. At the

same time, however, no studies have been conducted to examine the ways in which vegetation composition or density, or submerged plant litter, may affect LLFR larval-juvenile resting/hiding behaviors, resulting in a low rating for link understanding.

Finally, the CEM identifies several habitat elements with low- and medium-magnitude effects on one or more critical biological activities or processes. These include medium-magnitude effects of water chemistry on chemical stress and herbaceous vegetation on foraging. In addition, they include low-magnitude effects of water temperature on thermal stress, airborne contaminants on chemical stress; substrate dynamics and the hydrologic regime on mechanical stress, and substrate dynamics and the hydrologic regime on resting/hiding behaviors.

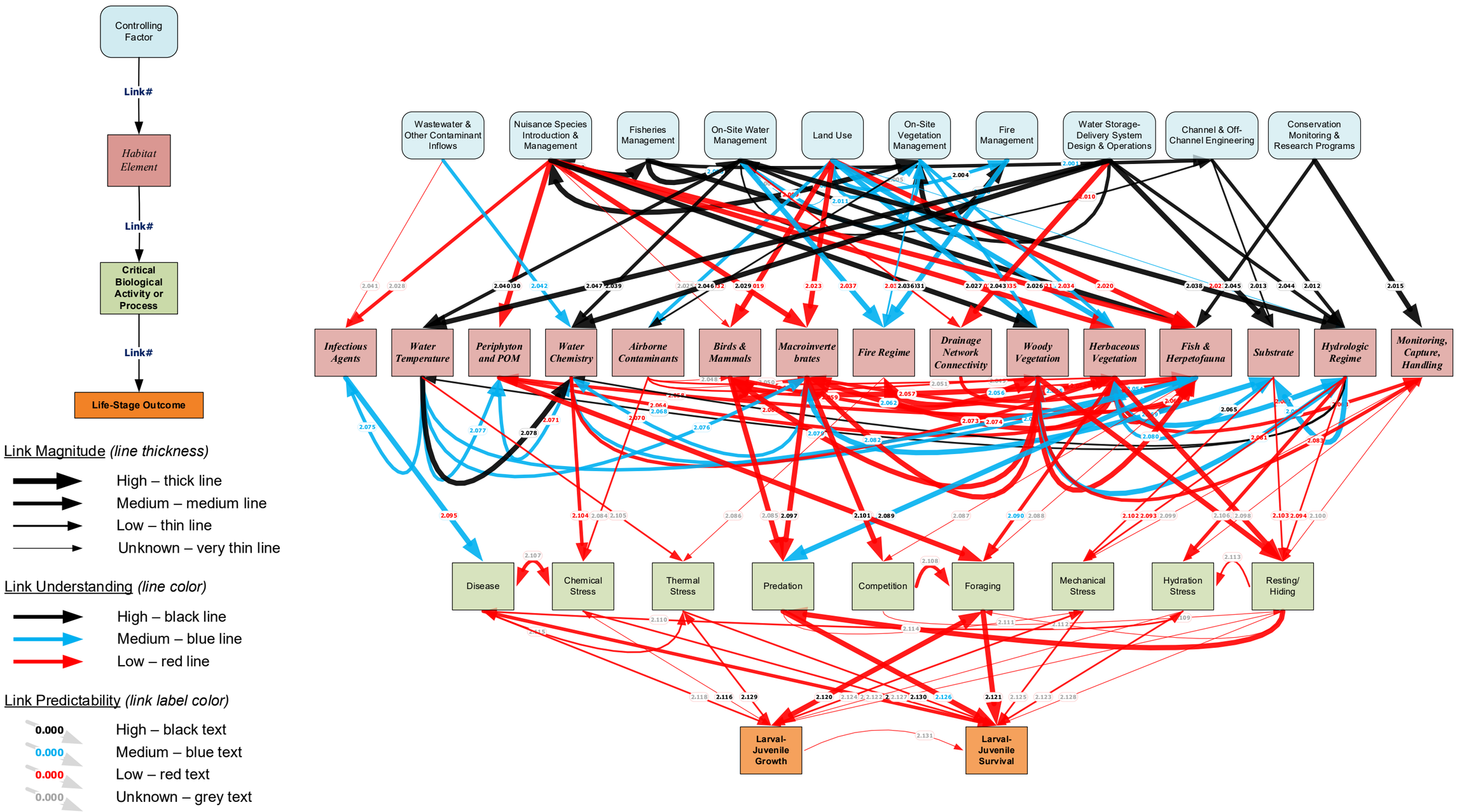

Figure 4.—CEM master diagram for LLFR life stage 2 – larvae and juveniles life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LLFR LIFE STAGE 3 – ADULTS

As described in chapter 2, this life stage begins with the completion of juvenile metamorphosis and lasts through the remainder of the frog's life. LLFR adults initially are sexually immature and reach sexual maturity only after additional growth and hormonal changes. The literature does not indicate how quickly LLFR adults may reach sexual maturity. The AZGFD (2006) reports unpublished data that "[t]he smallest males to exhibit secondary sexual characteristics from study sites in Graham and Yavapai counties, Arizona were 53.5 mm (2.1 in[ches]) and 56.2 mm (2.2 in[ches]) SVL, respectively." Platz (1988) reports adult sizes of 46–72 mm SVL among males and 53–87 mm SVL among females in general. LLFR adults live up to 3 years in the wild and may grow throughout their remaining lives (AZGFD 2006; Sredl et al. 1997a). This life stage has four life-stage outcomes (see figure 1): adult growth, adult survival, adult fertility, and gene flow. Figure 5 presents the complete CEM for this life stage, showing all controlling factors, habitat elements, critical biological activities and processes, life-stage outcomes, and their linkages.

The CEM proposes several interactions among the life-stage outcomes themselves for this life stage. Most significantly, the CEM proposes a high-magnitude effect of adult survival on fertility. The more adults that survive to full sexual maturity, and the more adults that survive to reproduce in multiple seasons, the greater the fertility of the population. However, no investigators have studied this effect specifically for LLFR or any closely related species.

Similar to the CEM for the preceding two life stages, the CEM for the adult life stage proposes that adult growth affects adult survival, but with unknown magnitude. The CEM also proposes that this particular link is bi-directional: The longer adults survive, the more they may grow. The literature for anurans in general indicates that larger adults have lower vulnerability to a range of threats and, therefore, results in a higher rate of survival. The relationship should be strong, based on core biological principles and observations of other anurans; however, no studies have been conducted to address the topic specifically for LLFR or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is rated as low. The CEM also proposes that adult growth affects fertility. Among anurans in general, larger males are more likely to attract mates, and larger females are more likely to produce larger egg masses. Again, however, no studies have addressed the topic specifically for LLFR or any closely related species; consequently, the magnitude of this link is unknown, and link understanding is rated as low. Finally, the CEM proposes that LLFR adult survival affects gene flow. Adults that live longer are more likely to contribute to gene flow by moving to other sites. But once again, no studies have been conducted to address the topic specifically for LLFR or any closely related species; consequently, the magnitude of this link is unknown, and link understanding is rated as low.

The CEM identifies nine critical activities or processes that directly affect adult LLFR survival; however, only two of these are proposed to have significant effects on this life-stage outcome: predation is proposed to have a high-magnitude effect, and disease is proposed to have a medium-magnitude effect.

Predation is the most commonly proposed cause of premature mortality among LLFR adults, contributing significantly (along with habitat loss) to LLFR extirpation across large areas of its historic range. The predators most commonly mentioned are the non-native American bullfrog and several non-native species of fishes. As discussed above (see this chapter, "Life Stage 2 – Larvae and Juveniles"), LLFR adults preferentially breed in shallower, low-velocity settings with relatively low densities—but not an absence—of herbaceous aquatic and riparian vegetation with partial woody canopy (see chapter 4). Such settings are less favored by many of the non-native predators of concern, which prefer deeper water and/or denser emergent aquatic vegetation. The AZGFD proposes that these aspects of LLFR habitat selection partially explain LLFR distribution along the Bill Williams River Valley (see chapters 3 and 4). However, it is not clear how much of this LLFR distribution results from LLFR habitat selection that reduces their interaction with these predators and how much is due to more intense removal of LLFR by predators in some settings versus others. As discussed below, LLFR adults also likely have a repertoire of behaviors for avoiding predators.

The literature on anurans in general provides a wide range of examples of the impacts of predation and the impacts of predator avoidance behaviors. In turn, the literature on LLFR emphasizes the overall importance of predation as a crucial factor in LLFR population dynamics rangewide, but it does not present formal evidence of predator-survival dynamics and only presents minimal information on predator-avoidance behaviors specifically for LLFR adults. The literature notes that knowledge of predation on LLFR is weak and is one of the major gaps in understanding the species and its conservation needs. Consequently, the causal link between predation and LLFR adult survival is rated as having low understanding.

The literature reports several instances of LLFR adult mortality—up to complete extirpation of a local population—as a result of illness, specifically red-leg or *Bd*. However, the literature also notes that such lethal outbreaks are associated with significant cold-weather events, in which the colder temperatures are beneficial to the pathogens and, perhaps, also reduce resistance among the LLFR in the affected pool. Such cold-weather events are likely infrequent along the LCR valley, which lies in the warmer (westernmost, lowest elevation) portion of the historic range of the species. Consequently, the CEM proposes that disease has only a medium-magnitude effect on LLFR adult survival. The lack of studies of the relationship results in a low rating for understanding of this proposed link.

Among the seven other critical activities or processes that are proposed to affect adult LLFR survival, five—chemical stress, foraging, hydration stress, mechanical stress, and thermal stress—are proposed to have low-magnitude effects and two—occupancy and inter-site movement and resting/hiding—are proposed to have unknown magnitudes of effect on survival. The CEM proposes that all these effects of critical activities or processes on adult survival have low understanding due to a lack of studies of these possible effects in LLFR or any closely related species. Note that, in contrast to the larval-juvenile life stage, foraging is proposed to have only a modest direct effect on survival in the present life stage. This difference arises because foraging success for adults directly affects adult growth, including adult health and body condition, and these in turn affect adult survival. As a result, foraging does affect adult survival, but indirectly through its effects on adult growth.

The CEM identifies eight critical activities or processes that directly affect adult LLFR growth; however, only one of these, foraging, is proposed to have significant effects on this life-stage outcome. Foraging success is a commonly recognized factor in growth and health in all animals; however, the literature provides extremely little information on LLFR adult foraging, such as information on food item selection, and no information on variability in foraging success. The literature emphasizes this gap in knowledge as a crucial area for investigation. On the other hand, the literature on leopard frogs in general amply documents an overwhelming preference for arthropod food items. In turn, the greater LCR ecosystem, particularly its riparian and wetland habitats, is home to a wide range of the general types of small arthropods on which adult leopard frogs are reported to feed. Further, field studies, such as those by the AZGFD along the Bill Williams, Big Sandy, Agua Fria, and Verde Rivers, indicate that, when present at all, LLFR always occur abundantly. These pieces of information suggest that LLFR adults do not suffer from foraging deficits in their preferred habitat settings. The link is proposed to be bi-directional: Larger and more mature LLFR adults are assumed to be more effective foragers. Nevertheless, the lack of direct evidence of LLFR adult foraging behaviors and preferences results in a low rating for link understanding.

The CEM identifies six critical activities or processes that directly affect LLFR adult fertility, three of which are proposed to have significant effects on this life-stage outcome. The CEM recognizes that, necessarily and with high magnitude, LLFR production of egg masses capable of successful incubation depends on adult success in mating and ovipositing; however, the literature provides no information on variability in LLFR mating or ovipositing success, or on factors that may affect it anywhere, let alone in the greater LCR ecosystem. Consequently, the link is assigned a low rating for understanding.

The CEM also proposes that chemical stress and thermal stress may both affect LLFR adult fertility, with medium magnitude. The literature indicates that LLFR can breed year round at geothermal springs but breed only during one or two

limited seasonal windows at sites that are not buffered from cool winter temperatures or hot summer temperatures; however, the LCR lies across the warmer, lower-elevation portion of the LLFR historic range, a portion in which winter air temperatures—and, therefore, in which winter water temperatures outside of the main Colorado River channel—are higher than across the rest of the historic range. As a result, LLFR in the LCR are less likely to experience thermal stress from cold conditions, and historic warm conditions appear to be within their range of tolerance. Similarly, the literature indicates that some forms of chemical stress (such as the effects of selenium or pesticide bioaccumulation) can alter reproductive fitness in frogs (Bank et al. 2007; Mann et al. 2009). Nevertheless, the lack of direct investigations of the effects of temperature and water chemistry on LLFR adult fertility results in a low rating for link understanding for both links.

Finally, the CEM proposes that two critical activities or processes directly affect gene flow between LLFR local populations. One of these, occupancy and inter-site movement, likely affects this life-stage outcome with high magnitude. The CEM proposes this necessary relationship based on basic biological principles and evidence from studies of gene flow among local populations in the Tucson area. However, no investigations have tracked actual inter-site movements among LLFR or calculated their effects on gene flow and genetic isolation anywhere, let alone within the greater LCR ecosystem.

The CEM proposes that several critical biological activities and processes affect each other, compounding their effects on LLFR life-stage outcomes. The CEM specifically identifies three links between critical biological activities and processes with likely high magnitudes, as follows:

- LLFR adult resting/hiding behaviors are proposed to affect the rate of predation on LLFR adults, with high magnitude. Sredl (2018) states that LLFR are cryptically colored and, in response to the presence of a possible predator, will sometimes remain motionless to escape detection by predators or alternatively will rely on saltation to escape to deep water or shoreline cover; however, the literature does not indicate how successful such behaviors may be against different kinds of predators. On the other hand, such behaviors are ubiquitous among frogs, and this warrants rating the proposed link as high magnitude. At the same time, however, the CEM necessarily rates understanding of the proposed link as low.

- The CEM proposes that competition from other species can affect the distribution of LLFR site occupancy across the landscape and the ability of LLFR adults to move successfully between sites. Occupation of large sections of the LCR valley by competitors such as the Rio Grande leopard frog appears to exclude LLFR and, consequently, also may act as barriers to LLFR inter-site movement. The facts of geography and biology seem to support this hypothesis, but in fact, no formal studies have been

conducted to examine the interactions of the two species In fact, many non-native species also appear to exclude LLFR from individual sites through predation (see below) and possibly habitat modification (crayfish) rather than through competition. Given the lack of investigation of how competition affects LLFR biogeography, the CEM necessarily rates understanding of the proposed link as low.

- The CEM proposes that predation also can affect the distribution of LLFR site occupancy across the landscape and the ability of LLFR adults to move successfully between sites. American bullfrogs, crayfish, and several non-native carnivorous fishes known to prey on LLFR occupy a substantial areas along the LCR valley, and their presence is described in the literature as having extirpated or having the potential to extirpate LLFR from these areas and, consequently, also act as barriers to LLFR inter-site movement through these areas. In fact, American bullfrogs, crayfish, and several non-native carnivorous fishes appear to have extirpated other leopard frogs across large portions of their original ranges in the Western United States; however, no formal studies have examined these interactions specifically for LLFR or any closely related species.

Other causal relationships among critical biological activities and processes with medium magnitude include a bi-directional cause-effect relationship between disease and chemical stress, and a uni-directional effect of competition on foraging. The CEM includes the relationship between disease and chemical stress because several studies of frog sensitivity to pollutants note that exposure can increase their sensitivity to disease as well; however, this has not been studied specifically for LLFR or any closely related species.

The CEM includes the relationship between competition and foraging because the abundance and range of species competing with LLFR adults for food should constrain LLFR adult prey selection and foraging success. Potential competitors with LLFR adults for food are abundant and ubiquitous in the LCR ecosystem; however, many of these competitors are native species among which LLFR have evolved and, therefore, likely have adaptations to reduce the magnitude of the effect, such as through resource partitioning. On the other hand, some non-native competitors with LLFR adults may pose bigger challenges because LLFR adaptations to competition may not be as effective against non-native competitors. The subject has not been studied for LLFR or any closely related species in the region, although reports identify competition from the Rio Grande leopard frog as a possible example.

The CEM identifies several habitat elements with high-magnitude direct effects on one or more critical biological activities or processes for LLFR adults, as follows:

- The CEM proposes that water temperature or its pattern of variation strongly affects LLFR mating and ovipositing. LLFR reportedly can mate year round at geothermal springs, and the timing of LLFR mating at all other types of locations matches the timing of changes in air (and, therefore, in water) temperatures. The cumulative evidence in the literature appears to support an inference that temperature plays an important role in cueing LLFR mating; however, no investigators have specifically studied the correlation of LLFR mating with changes in air temperature. The CEM also notes that the LCR lies at the western edge and lowest elevations of the LLFR historic range, which is the climatically warmest part of that range. Thermal constraints on LLFR mating, therefore, may be weaker in the LCR ecosystem than elsewhere in the LLFR historic range.

- The CEM proposes that the composition and density of the bird and mammal assemblages strongly affect the rate of predation on LLFR adults. Several wetland birds and mammals in the LCR ecosystem may prey on adult LLFR (see chapter 3, "Predation"). Consequently, the taxonomic, functional, and size composition; spatial and temporal distribution; abundance; and activity levels of the bird and mammal assemblages could affect the rate of predation that LLFR adults face. However, different birds and mammals may prey on LLFR adults in different ways and/or to different degrees, and they may also compete with each other. Knowledge is very limited concerning which birds and mammals prey on LLFR, but such predation is extremely likely to occur at a high rate and to take place throughout the year in all locations, constrained only by the effects of other habitat elements on predator activity.

- The CEM proposes that the composition and density of the fish and herpetofauna assemblages strongly affect the rate of predation on LLFR adults. Garter snakes, and possibly other snakes, may prey on LLFR adults (see chapter 3, "Predation"), and American bullfrogs eat smaller adult frogs (and smaller adult bullfrogs, too [USFWS 2017]). Consequently, the taxonomic, functional, and size composition; spatial and temporal distribution; abundance; and activity levels of the herpetofauna assemblage necessarily affects the rate of predation that LLFR adults face. However, different fishes and herpetofauna may prey on LLFR adults in different ways and/or to different degrees, and they may also compete with each other. Knowledge is very limited concerning which reptiles or amphibians may prey on LLFR other than garter snakes and bullfrogs. Bullfrogs may not always occur in locations inhabited by LLFR, and vice versa, as indicated by AZGFD surveys along the Bill Williams River Valley, but garter snakes appear to be ubiquitous (again, see AZGFD survey results for the Bill Williams River Valley) and highly effective predators of LLFR. As a result, predation on LLFR adults by members of the herpetofaunal assemblage is extremely likely to occur at a high rate and to take place throughout the year in all locations, constrained only by the effects of other habitat elements on herpetofaunal predator activity.

- The CEM proposes that the composition and density of the macroinvertebrate assemblage strongly affect LLFR adult foraging success. LLFR adults are thought to consume a broad range of arthropods. Consequently, the taxonomic, functional, and size composition; spatial and temporal distribution; abundance; and activity levels of the macroinvertebrate assemblage could affect LLFR adult foraging options and rates of success. While LLFR adult success in feeding on any one particular macroinvertebrate prey item may be unpredictable (e.g., varying with the abundance and ecology of each potential prey item), LLFR adult foraging success overall should vary predictably with the richness and density of macroinvertebrates in the appropriate size range. Foraging behavior and food selection among leopard frogs in general, especially the northern leopard frog, provide a basis for inferences about LLFR, but foraging behavior among LLFR adults has never been studied systematically, and the literature identifies this as a major knowledge gap.

- The CEM proposes that drainage network connectivity (as defined in chapter 4) strongly affects LLFR site occupancy and inter-site movement. The literature strongly suggests that LLFR inter-site movement occurs mostly or entirely along drainage network lines (see chapters 3 and 4). As a result, any degradation in drainage network connectivity could impair LLFR inter-site movement; however, no analyses have been conducted on drainage network connectivity and its capacity to support or inhibit LLFR inter-site movement within the greater LCR ecosystem. The dams along the portions of the main stem LCR where LLFR potentially could occur (e.g., Parker Dam, Imperial Dam), and similarly on the Bill Williams River (Alamo Dam), likely do limit LLFR inter-site movement at this large scale; however, LLFR may face fewer barriers at more local scales within the greater LCR ecosystem, particularly given the modest but not insignificant overland distances they seem to be able to traverse during inter-site movement. Even small puddles, including puddles in cattle hoof prints, may provide "stepping stones" for LLFR adult inter-site movement. On the other hand, again, no studies have assessed the matter for LLFR in the greater LCR ecosystem. As a result, the CEM assigns a rating of low for link understanding.

- The CEM proposes that the compositions and densities of both the herbaceous and woody vegetation assemblages in and around aquatic and wetland sites occupied by LLFR strongly affect mating and ovipositing behaviors and success at these sites. AZGFD studies of LLFR breeding site preferences along the LCR, Bill Williams River, Agua Fria River, and Verde Rivers demonstrate that LLFR adults oviposit significantly less often in dense herbaceous vegetation or under dense woody canopy. Dense stands of herbaceous vegetation moderately common and dense stands of woody vegetation, particularly saltcedar, are very common in the LCR ecosystem. The AZGFD noted its inability to survey locations with

dense herbaceous and/or woody vegetation during its study of current and potential LLFR habitat availability in the LCR and Bill Williams River valleys (see chapters 3 and 4). The AZGFD authors of studies along the LCR, Bill Williams River, Agua Fria River, and Verde River valleys did not analyze their data to try to quantify an optimal range of emergent herbaceous vegetation or woody canopy densities for LLFR habitat or breeding site selection. However, Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014) note that, when present at high densities, cattail, bulrush, and common reed in particular reduce habitat quality for LLFR. Rosen et al. (2013) also recommend that habitat creation for native leopard frogs avoid fast-growing herbaceous species such as cattails and bulrushes because, without intensive management, they form dense stands that native leopard frogs tend to avoid. Given the quantity and quality of data collected by the AZGFD on LLFR breeding site selection along the LCR, Bill Williams River, Agua Fria River, and Verde River valleys, these two links are rated as high for understanding.

- The CEM proposes that the composition and densities of both the herbaceous and woody vegetation assemblages in and around aquatic and wetland sites occupied by LLFR also strongly affect resting/hiding behaviors and success at these sites. Surveys by the AZGFD on behalf of the LCR MSCP along the LCR and in the Bill Williams River watershed statistically demonstrate that LLFR select locations for resting and hiding with greater aquatic vegetative cover immediately overhead and greater canopy cover along the nearest shoreline compared to average conditions at these aquatic-wetland sites (Cotten and Leavitt 2014; Leavitt et al. 2017). These findings confirm anecdotal records that LLFR preferentially select microhabitats for resting and hiding with emergent aquatic vegetative cover and nearby littoral canopy cover (AZGFD 2006; Sredl 2018; Swann and Wallace 2010). Although the AZGFD investigators note specifically that high densities of saltcedar reduce habitat quality for LLFR, the report authors did not analyze their data to try to quantify an optimal range of herbaceous cover or canopy densities for LLFR habitat. Consequently, the CEM assigns these two links a medium rating for understanding. (The AZGFD also noted its inability to survey locations with dense vegetation during its study of current and potential LLFR habitat availability in the LCR and Bill Williams River valleys.)

- The CEM proposes that substrate conditions at aquatic and wetland sites occupied by LLFR also strongly affect resting/hiding behaviors and success at these sites. The literature indicates that LLFR do not have strong preferences for substrate type(s), such as silt versus sand versus gravel, at sites they occupy versus those they do not. However, LLFR evolved in a natural system with occasional high-flow, substrate-disturbing events from spring rains and snowmelt, and summer rains. The repertoire of behaviors they appear to have evolved for coping

with these conditions include actively seeking resting/hiding habitat consisting of lower-velocity/less turbulent habitat settings such as refuges in banks, under debris piles, and in the substrate during individual flow pulses. At the same time, the CEM notes that episodes of high-velocity or high-turbulence, substrate-disturbing flows in the present-day, regulated LCR ecosystem are localized, brief, and well within the abilities of LLFR to tolerate and, therefore, probably do not test the limits of LLFR behaviors for responding in the face of such conditions. The CEM also notes that, while it includes increasing documentation of substrate conditions at sites occupied by LLFR, this literature does not provide sufficient details to warrant a rating of high for understanding.

- The CEM notes that monitoring activities at aquatic and wetland sites occupied by LLFR can strongly affect resting/hiding behaviors at these sites, and vice versa. Specifically, AZGFD reports on its studies in the greater LCR ecosystem and along the Agua Fria and Verde River valleys consistently note that VES monitoring activity causes LLFR adults to seek cover (i.e., triggers hiding activity; see chapters 3 and 4). In turn, LLFR adult hiding activity can reduce LLFR adult visibility during VESs. The AZGFD cites this pattern as one reason why monitoring teams may supplement VES with dip netting, CR, FTAs, and DARs (i.e., to help overcome the effects of LLFR behavior on the effectiveness of simple VES methods). Several publications in fact document the effects of resting/hiding behavior on the effectiveness of different monitoring methods not only for LLFR specifically but among southwestern leopard frogs in general, and they also document the effects of this interaction on investigator decisions about monitoring methods. The detailed documentation in AZGFD reports supports a rating of high for link understanding.

- The CEM proposes that the composition and densities of both the herbaceous and woody vegetation assemblages also strongly affect LLFR site occupancy itself. Specifically, the AZGFD studies of LLFR occupancy preferences along the LCR, Bill Williams River, Agua Fria River, and Verde River valleys demonstrate that LLFR adults avoid sites with dense vegetation. As noted above (see effects of vegetation on mating and ovipositing), dense stands of herbaceous vegetation moderately common and dense stands of woody vegetation, particularly saltcedar, are very common in the LCR ecosystem. The AZGFD authors of studies did not analyze their data to try to quantify an optimal range of vegetation densities for LLFR site occupancy; however, Cotten (2011) and others (Cotten and Grandmaison 2013; Cotten and Leavitt 2014) note that, when present at high densities, cattail, bulrush, common reed, and saltcedar in particular, reduce habitat quality for LLFR. Rosen et al. (2013) also recommend that habitat creation for native leopard frogs avoid fast-growing herbaceous species such as cattails and bulrushes because,

without intensive management, they form dense stands that native leopard frogs tend to avoid. The detailed documentation in AZGFD reports supports a rating of high for link understanding.

- The CEM notes that details of the local hydrologic regime strongly affect LLFR site occupancy. Specifically, LLFR adults respond to drying conditions at an occupied site either by (a) by seeking refuge in cracks in the substrate, in burrows, and under debris piles or (b) moving out to find a suitable alternative site nearby. Conversely, surface sites with water that persists year round, or at least for all but the summer season, will attract and retain LLFR occupancy in the absence of some catastrophe that makes the site otherwise unusable by LLFR. The CEM notes that water levels in many water bodies along the LCR (but not along the Bill Williams River below Alamo Dam) are regulated to ensure stable water levels or flows, and this may maintain a high level of water permanence at a large number of locations and, as a corollary, reduce the geographic extent and frequency at which drying out at a site triggers inter-site movement by LLFR adults seeking alternative habitat. However, there are two important gaps in relevant knowledge: (1) The literature does not indicate how long LLFR can persist in refuges at a site that has dried out (i.e., for semipermanent water bodies, how long or often can water be absent). (2) The actual role of drying down at sites in triggering LLFR movement to other sites has not been studied, and the relationship posited here rests on studies of Chiricahua leopard frogs. The CEM therefore assigns a rating of medium for understanding of the link between the hydrologic regime and LLFR site occupancy and inter-site movement.

Finally, the CEM identifies several habitat elements with low- and medium-magnitude effects on one or more critical biological activities or processes for LLFR adults. These include medium-magnitude effects of water chemistry on chemical stress, macroinvertebrates and fish and herpetofauna on competition, and herbaceous vegetation on foraging. In addition, they include low-magnitude effects of water temperature on thermal stress, airborne contaminants on chemical stress, substrate dynamics and the hydrologic regime on mechanical stress, hydrologic regime on hydration stress and on mating and ovipositing, and fish and herpetofauna on hybridization.

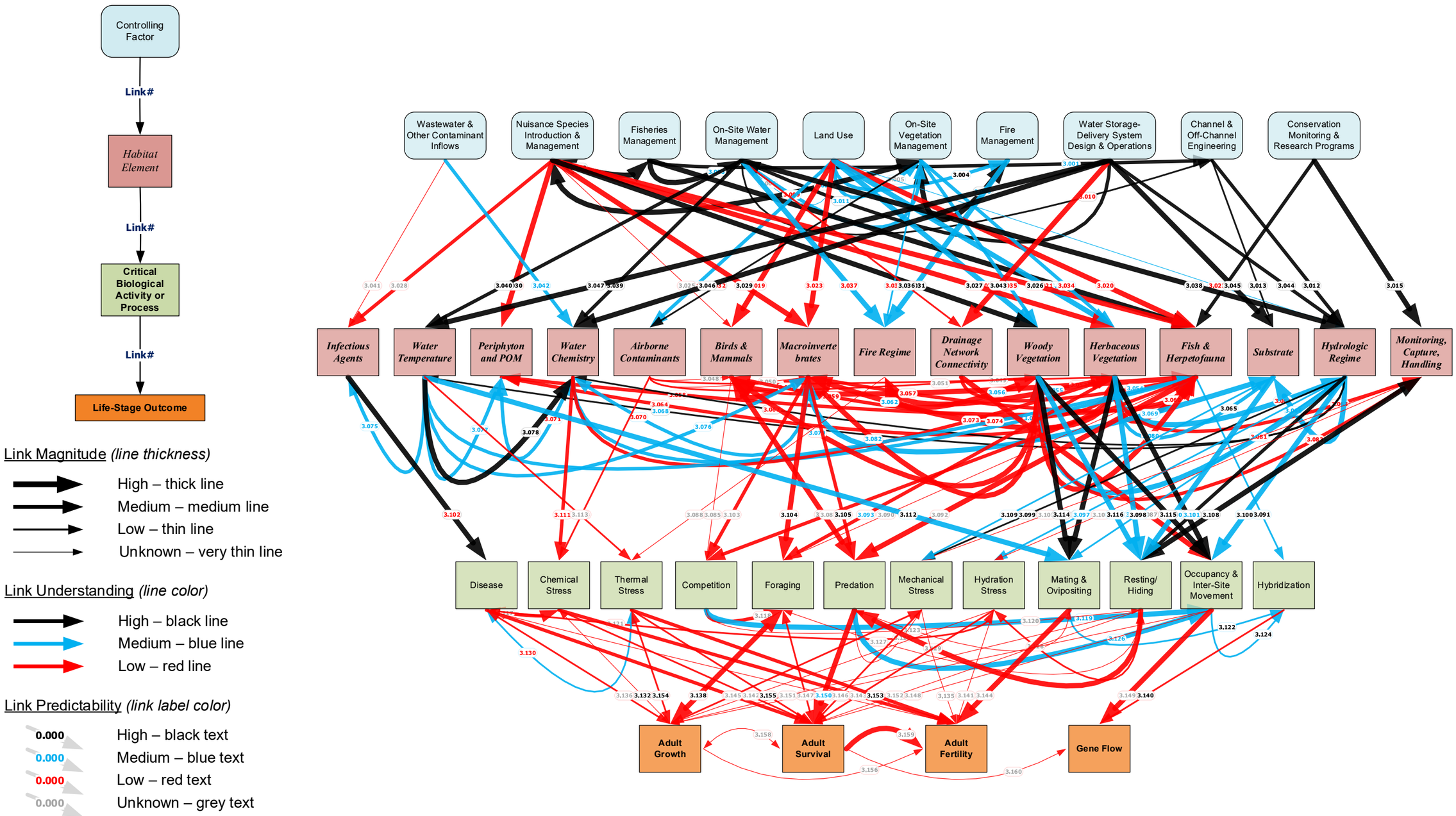

Figure 5.—CEM master diagram for LLFR life stage 3 – adult life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

Chapter 7 – Causal Relationships Across All Life Stages

This chapter examines the information assembled for the CEM across all life stages to assess the following:

- Which critical biological activities and processes most strongly affect the life-stage outcomes across all life stages?
- Which critical biological activities and processes strongly affect other critical biological activities and processes across all life stages?
- Which habitat elements, through their abundance, distribution, and/or quality, most strongly affect the most influential activities and processes across all life stages?
- Which habitat elements, through their abundance, distribution, and/or quality, most strongly affect the abundance, distribution, and/or quality of other habitat elements across all life stages?
- Which controlling factors most strongly affect the most influential habitat elements across all life stages?
- Which of the most influential causal relationships appear to be the least understood in ways that could affect their management?

EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON LIFE-STAGE OUTCOMES

Table 7 shows which critical biological activities and processes directly affect each life-stage outcome, the estimated magnitude of each effect, and the estimated level of understanding of the effect. Four critical biological activities or processes—chemical stress, disease, hydration stress, mechanical stress, predation, and thermal stress—directly affect at least one life-stage outcome in every life stage. Two critical biological activities or processes—foraging and resting/hiding—directly affect life-stage outcomes for the larval-juvenile and adult life stages but not for the egg life stage. Two critical biological activities or processes—hybridization, and mating and ovipositing—only affect one life stage, adults.

Table 7.—Direct effects of critical biological activities and processes on LLFR life-stage outcomes

Letter in cell indicates: ***H*** = high; **M** = medium; L = low; *U* = unknown.
Letter color indicates the level of understanding of the effect: Low = **X**

Life-stage outcome ➔ / **Critical biological activity or process 🡻**	**Egg growth**	**Egg survival**	**Larval-juvenile growth**	**Larval-juvenile survival**	**Adult fertility**	**Adult growth**	**Adult survival**	**Gene flow**
Chemical stress	*U*	L	*U*	L	**M**	*U*	L	
Disease	*U*	L	L	**M**	*U*	L	**M**	
Foraging			***H***	***H***		***H***	L	
Hybridization								L
Hydration stress	*U*	L	*U*	L	*U*	*U*	L	
Mating and ovipositing					***H***			
Mechanical stress	L	L	L	L	*U*	L	L	
Occupancy and inter-site movement		L				*U*	*U*	***H***
Predation		***H***		***H***			***H***	
Resting/hiding			*U*	*U*		*U*	*U*	
Thermal stress	L	L	L	L	**M**	L	L	

Table 7 indicates that only four critical biological activities or processes are proposed to have high-magnitude effects on any life-stage outcome in any life stage. Foraging is proposed to affect larval-juvenile growth, larval-juvenile survival, and adult growth with high magnitude. Mating and ovipositing is proposed to affect adult fertility with high magnitude. Occupancy and inter-site movement is proposed to affect gene flow with high magnitude. Predation is proposed to affect survival with high magnitude for all three life stages. The CEM assigns a rating of low for link understanding (red letters in table) to all of these proposed high-magnitude relationships and, in fact, to every link shown in table 7, indicating a lack of knowledge about most aspects of LLFR biology.

Table 7 also indicates that only three critical biological activities or processes are proposed to have medium-magnitude effects on any life-stage outcome in any life stage. Chemical stress is proposed to have a medium potential to affect adult

fertility. Disease is proposed to have a medium potential to affect larval-juvenile and adult survival. Thermal stress is proposed to have a medium potential to affect adult fertility. All other links shown in table 7 are proposed to have either low or unknown magnitude effects.

Looked at another way, table 7 indicates that the CEM identifies predation as the most important critical biological activity or process shaping egg survival; foraging as the most important critical biological activity or process shaping larval-juvenile growth; foraging and predation as the most important critical biological activities or processes shaping larval-juvenile survival, with secondary effects from disease; mating and ovipositing as the most important critical biological activity or process shaping adult fertility, with secondary effects from chemical stress and thermal stress; foraging as the most important critical biological activity or process shaping adult growth; predation as the most important critical biological activity or process shaping adult survival, with secondary effects from disease; and occupancy and inter-site movement as the most important critical biological activity or process shaping gene flow.

EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON EACH OTHER

Table 8 shows which critical biological activities and processes directly affect other critical biological activities and processes, thereby influencing life-stage outcomes indirectly across the three LLFR life stages; the estimated magnitude of these effects; and the estimated level of understanding of the effects. Nine critical biological activities or processes directly affect at least one other critical biological activity or process in at least one life stage; however, only five critical biological activities or processes—chemical stress, disease, hydration stress, predation, and thermal stress—are proposed to affect one or more other critical biological activities or processes in all three life stages. Two critical biological activities or processes—competition and resting/hiding—affect one or more other critical biological activities or processes in both the larval-juvenile and adult life stages but none in the egg life stage. Three critical biological activities or processes—hybridization, mating and ovipositing, and occupancy and inter-site movement—only pertain to the adult life stage and, therefore, are affected by other critical biological activities or processes only in this life stage. Three critical biological activities or processes—foraging, hybridization, and mechanical stress—do not affect any other critical biological activities or processes in any life stage.

Table 8.—Direct effects of critical biological activities and processes on each other across the three LLFR life stages

The three characters in each cell indicate the ratings for egg, larval-juvenile, and adult life stages, from top to bottom, respectively
Letter in cell indicates proposed link magnitude: ***H*** = high; **M** = medium; L = low; *U* = unknown.
Letter color indicates the level of understanding of the effect: High = **X**; Medium = **X**; Low = **X**

Affected critical biological activity or process ➔ **Causal critical biological activity or process 🡻**	**Chemical stress**	**Competition**	**Disease**	**Foraging**	**Hybridization**	**Hydration stress**	**Mating and ovipositing**	**Mechanical stress**	**Occupancy and inter-site movement**	**Predation**	**Resting/hiding**	**Thermal stress**
Chemical stress			*U* **M** **M**									
Competition				- **M** **M**					- - ***H***		- *U* *U*	
Disease	*U* **M** **M**											L L L
Foraging												
Hybridization												
Hydration stress			*U* L L								- L L	
Mating and ovipositing					- - L					- - *U*		
Mechanical stress												
Occupancy and inter-site movement					- - L							
Predation							- - *U*	*U* *U* *U*	- - ***H***			
Resting/hiding				- *U* *U*		- L L				- **M** **M**		
Thermal stress			L L L									

The CEM proposes that most of the effects of critical biological activities and processes on each other have low or unknown magnitudes, with low understanding. The exceptions that stand out from this overall pattern are as follows:

- Chemical stress and disease are proposed to have medium-magnitude effects on each other in the larval-juvenile and adult life stages.
- Competition is proposed to have medium-magnitude effects on foraging success in the larval-juvenile and adult life stages.
- Competition and predation are both proposed to have high-magnitude effects on occupancy and inter-site movement for LLFR adults, with high levels of understanding.
- The effects of disease and thermal stress on each other are proposed to have a medium level of understanding for the adult life stage but only low understanding for the other two life stages.
- The effects of mating and ovipositing, and of occupancy and inter-site movement on hybridization, are proposed to have a medium level of understanding.
- Resting/hiding behaviors are proposed to have a cumulative medium-magnitude effect on predation rates for the larval-juvenile and adult life stages.

EFFECTS OF HABITAT ELEMENTS ON CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES

Table 3 (see chapter 4) identifies which habitat elements affect which critical biological activities and processes across all LLFR life stages. These relationships are in fact largely identical across all life stages in the CEM; however, a small number of critical biological activities and processes—and, therefore, a small number of habitat elements—only come into play for one or two life stages. Table 9 shows which habitat elements directly affect which critical biological activities and processes, as in table 3, and also indicates the proposed magnitude and level of understanding of these effects among the three LLFR life stages. The key for table 9 is the same as for table 8.

Roughly half the entries in table 9 indicate effects of habitat elements on critical biological activities and processes with low or unknown magnitude. Conversely,

Table 9.—LLFR habitat elements and the critical biological activities and processes they are proposed to directly affect across the three LLFR life stages
(See table 8 for key.)

Affected critical biological activity or process ➔ **Causal habitat elements 🡻**	**Chemical stress**	**Competition**	**Disease**	**Foraging**	**Hybridization**	**Hydration stress**	**Mating and ovipositing**	**Mechanical stress**	**Occupancy and inter-site movement**	**Predation**	**Resting/hiding**	**Thermal stress**
Airborne contaminants	L L L											
Birds and mammals		- - *U*								***H*** ***H*** ***H***		
Drainage network connectivity									- - ***H***			
Fire regime												*U* *U* *U*
Fish and herpetofauna		- **M** *U*		- *U* *U*	- - L					***H*** ***H*** ***H***		
Herbaceous vegetation				- **M** **M**			- - ***H***		- - ***H***		- ***H*** ***H***	
Hydrologic regime						**M** **M** L	- - L	**M** L L	- - ***H***		- L **M**	
Infectious agents			***H*** ***H*** ***H***									
Macroinvertebrates		- ***H*** **M**		- - ***H***						***H*** ***H*** **M**		
Monitoring, capture, handling						*U* *U* *U*		*U* *U* *U*			- *U* ***H***	
Periphyton and particulate organic matter (POM)				- ***H*** -								
Substrate								L L L			- L ***H***	
Water chemistry	**M** **M** **M**											
Water temperature							- - ***H***					L L L
Woody vegetation							- - ***H***		- - ***H***		- ***H*** ***H***	

table 9 indicates several effects of habitat elements on critical biological activities and processes with high or medium magnitude, as follows. Specifically, the CEM proposes that:

- The composition and density of the bird and mammal assemblages affect the rate of predation on LLFR in all three life stages with high magnitude; however, understanding of these relationships is rated low for all three life stages.

- The composition and density of the fish and herpetofauna assemblages are proposed to have a medium-magnitude but poorly understood effect on the rate of competition experienced by LLFR larvae and juveniles.

- The composition and density of the fish and herpetofauna assemblages affect the rate of predation experienced by LLFR in all three life stages with high magnitude. The relationship is proposed to have a medium level of understanding for the LLFR larval-juvenile life stage but a low level of understanding for the egg and adult life stages.

- The composition and density of the herbaceous vegetation assemblage, particularly aquatic (i.e., emergent) herbaceous vegetation, affect foraging behaviors by LLFR larvae and adults with medium magnitude, although understanding of these relationships is rated as low. The composition and density of the herbaceous vegetation assemblage also is proposed to affect mating and ovipositing behaviors and occupancy and inter-site movement by LLFR adults with high magnitude. Understanding of these two relationships is rated as high. Finally, the composition and density of the herbaceous vegetation assemblage are proposed to affect resting/hiding behavior by LLFR larvae and adults with high magnitude. The CEM rates understanding as low for the latter effects for LLFR larvae and medium for LLFR adults.

- The hydrologic regime has medium-magnitude effects on the incidence of hydration stress among LLFR eggs and larvae and the incidence of mechanical stress among LLFR eggs. All three links are rated low for understanding. In turn, the CEM proposes that the hydrologic regime has moderately well understood, high-magnitude effects on LLFR occupancy and inter-site movement and well understood, medium-magnitude effects on LLFR adult resting/hiding behavior.

- Infectious agents have high-magnitude effects on disease in all three life stages, but the level of understanding of these relationships varies among the life stages. The CEM rates this understanding as low for the LLFR egg stage, medium for the LLFR larval-juvenile life stage, and high for the LLFR adult life stage.

- The composition and density of the macroinvertebrate assemblage have high-magnitude effects on the level of competition experienced by LLFR larvae, foraging success among LLFR adults, and the rate of predation experienced by LLFR eggs and larvae-juveniles. At the same time, the CEM proposes that the composition and density of the macroinvertebrate assemblage have medium-magnitude effects on the level of competition experienced by LLFR adults and the rate of predation experienced by these adults. The CEM also notes that these relationships are poorly understood.

- Monitoring, capture, and handling activities across LLFR habitat have high-magnitude effects on LLFR adult resting/hiding behaviors, and these effects are well understood.

- The composition and density of periphyton and POM have high-magnitude effects on LLFR larval foraging, but these relationships are poorly understood.

- The texture and stability of the substrate affect LLFR adult resting/hiding behavior, and these effects are moderately well understood.

- Water chemistry has medium-magnitude effects on the incidence of chemical stress across all three life stages, but these effects are poorly understood.

- Water temperature has high-magnitude effects on LLFR mating and ovipositing, and these effects are moderately well understood.

- The composition and density of the woody vegetation assemblage affect mating and ovipositing behaviors, and occupancy and inter-site movement by LLFR adults, with high magnitude. Understanding of these two relationships is rated as high. Finally, the composition and density of the woody vegetation assemblage are proposed to affect resting/hiding behavior by LLFR larvae and adults with high magnitude. The CEM rates understanding as low for the latter effects for LLFR larvae and medium for LLFR adults.

EFFECTS OF HABITAT ELEMENTS ON EACH OTHER

Table 4 (see chapter 4) identifies which habitat elements affect other habitat elements. These relationships are identical across all three LLFR life stages. Table 10 shows which habitat elements directly affect which other habitat elements, as in table 4, and also indicates the proposed magnitude and level of understanding of these effects among the three LLFR life stages.

Table 10.—Direct effects of habitat elements on each other across the three LLFR life stages (See table 8 for key.)

Affected habitat element ➔ / Causal habitat elements ➓	Airborne contaminants	Birds and mammals	Drainage network connectivity	Fire regime	Fish and herpetofauna	Herbaceous vegetation	Hydrologic regime	Infectious agents	Macroinvertebrates	Monitoring, capture, handling	Periphyton and particulate organic matter (POM)	Substrate	Water chemistry	Water temperature	Woody vegetation
Airborne contaminants		*U*				L			*U*						L
Birds and mammals					***H***	M			***H***						***H***
Drainage network connectivity					M										
Fire regime						***H***									***H***
Fish and herpetofauna		***H***							M		M				
Herbaceous vegetation		M		***H***	***H***		***H***		***H***	M	M	M			
Hydrologic regime						***H***						***H***	L	L	***H***
Infectious agents															
Macroinvertebrates		*U*			M	***H***						***H***	M		***H***
Monitoring, capture, handling															
Periphyton and particulate organic matter (POM)					M								M		
Substrate						M			***H***						
Water chemistry					M	M			M		M				
Water temperature					M			M	M		M		***H***		
Woody vegetation		***H***		***H***	***H***		***H***		***H***	M					

Table 10 shows that only two habitat elements—infectious agents and monitoring, capture, handling—have no direct effects on any others. Further, all other habitat elements, except airborne contaminants, have a medium- or high-magnitude effect on at least one other habitat element. High-magnitude effects of habitat elements on other habitat elements are as follows. Specifically, the CEM proposes that:

- The composition and densities of the bird and mammal assemblages both affect and are affected by the composition and densities of the fish and herpetofauna assemblages, and the woody vegetation assemblage, with high magnitude. The composition and densities of the bird and mammal assemblages also affect the macroinvertebrate assemblage, but the feedback effects of the macroinvertebrate assemblage on the bird and mammal assemblages are unknown. All of these relationships are proposed to have low understanding.

- The fire regime affects the compositions and densities of both the herbaceous and woody vegetation assemblages, and vice versa, with high magnitude, but the relationships are proposed to have low understanding.

- The composition and density of the herbaceous vegetation assemblage, particularly for aquatic herbaceous vegetation, also affects the fish and herpetofauna assemblages with high magnitude (and the bird and mammal assemblage with medium magnitude); however, the relationships are proposed to have low understanding.

- The compositions and densities of the herbaceous vegetation assemblage, particularly aquatic herbaceous vegetation, and the woody vegetation assemblage both affect and are affected by the composition and density of the macroinvertebrate assemblage with high magnitude; however, the relationships also are proposed to have low understanding.

- The hydrologic regime both affects and is affected by the compositions and densities of the herbaceous vegetation assemblage, particularly aquatic herbaceous vegetation, and the woody vegetation assemblage with high magnitude. These two pairs of reciprocal relationships are all proposed to have medium understanding.

- Both the hydrologic regime and the composition and density of the aquatic macroinvertebrate assemblage affect the texture and stability of the substrate, with high magnitude, and these relationships are proposed to have medium understanding. The texture and stability of the substrate reciprocally also affect the composition and density of the aquatic macroinvertebrate assemblage with high magnitude. These relationships are all proposed to have medium understanding.

- Finally, water temperature affects water chemistry with high magnitude and involves several well-understood causal relationships.

EFFECTS OF CONTROLLING FACTORS ON HABITAT ELEMENTS

Table 6 in chapter 5 identifies which controlling factors affect which habitat elements in the LLFR conceptual ecological model. These relationships are identical across all life stages in the CEM. Table 11 also presents this information but adds information on the magnitude and level of understanding of these effects.

Table 11.—Direct effects of controlling factors on habitat elements across the three LLFR life stages (See table 8 for key.)

Habitat elements ➔ / Controlling factors ⬇	Airborne contaminants	Birds and mammals	Drainage network connectivity	Fire regime	Fish and herpetofauna	Herbaceous vegetation	Hydrologic regime	Infectious agents	Macroinvertebrates	Monitoring, capture, handling	Periphyton and particulate organic matter (POM)	Substrate	Water chemistry	Water temperature	Woody vegetation
Channel and off-channel engineering							M					L			
Conservation monitoring and research programs					M					***H***					
Fire management				***H***											
Fisheries management					***H***										
Land use	M	***H***			***H***	***H***	*U*		***H***						***H***
Nuisance species introduction and management		*U*			***H***	***H***		M	***H***		***H***				***H***
Onsite vegetation management	L			L		M									M
Onsite water management			L	***H***			***H***						M	M	
Wastewater and other contaminant inflows								*U*					M		
Water storage-delivery system design and operations			***H***				M					***H***	***H***	***H***	

Table 11 shows that 7 of the 10 controlling factors—conservation monitoring and research programs, fire management, fisheries management, land use, nuisance species introduction and management, onsite water management, and water storage-delivery system design and operations—has a high-magnitude effect on at least 1 habitat element. These high-magnitude effects of habitat elements on other habitat elements are as follows. Specifically, the CEM proposes that:

- Conservation monitoring and research programs, by definition, have a high-magnitude effect on monitoring, capture, and handling. This relationship is well understood.

- Fire management affects the fire regime. This relationship is proposed to have medium understanding in the greater LCR ecosystem.

- Fisheries management, by definition, has a high-magnitude effect on the composition and density of the fish assemblage. This relationship is well understood.

- Land use patterns and practices have high-magnitude, moderately well understood effects on the composition and densities of the herbaceous and woody vegetation assemblages. In turn, land use patterns and practices have high-magnitude but only poorly understood effects on the composition and densities of the bird and mammal, fish and herpetofauna, and macroinvertebrate assemblages.

- Nuisance species introduction and management have high-magnitude but poorly understood effects on the fish and herpetofauna, herbaceous vegetation, macroinvertebrate, periphyton and POM, and woody vegetation assemblages. The CEM proposes that the effects of nuisance species introduction and management on the bird and mammal assemblages are unknown and poorly understood.

- Onsite water management has high-magnitude, moderately well understood effects on the fire regime and well-understood effects on the hydrologic regime.

- Finally, water storage-delivery system design and operations have high-magnitude effects on drainage network connectivity in the LCR ecosystem; however, no studies have been conducted to investigate water storage-delivery system design and operations in the greater LCR ecosystem for their possible effects on ecological connectivity; these possible effects, therefore, are rated as having low understanding. At the same time, water storage-delivery system design and operations have high-magnitude, well-understood effects in the LCR ecosystem on substrates, water chemistry, and water temperatures.

The CEM also recognizes that several controlling factors directly affect other controlling factors. Table 12 shows which controlling factors affect which others, with what proposed magnitude, and with what proposed level of understanding. Table 12 shows that four controlling factors have high-magnitude effects on other controlling factors, as follows. Specifically, the CEM proposes that:

- Fire management has high-magnitude, well-understood effects on onsite vegetation management, and vice versa.
- Fisheries management has high-magnitude, well-understood effects on nuisance species introduction and management, and vice versa.
- Fisheries management has high-magnitude, well-understood effects on onsite water management.
- Finally, nuisance species introduction and management has high-magnitude, well-understood effects on onsite vegetation management, and vice versa.

Table 12.—Direct effects of controlling factors on each other across the three LLFR life stages (See table 8 for key.)

Affected controlling factor ➔ / Causal controlling factor ⬇	Channel and off-channel engineering	Fire management	Fisheries management	Land use	Nuisance species introduction and management	Onsite vegetation management	Onsite water management	Water storage-delivery system design and operations
Channel and off-channel engineering								
Fire management						***H***		
Fisheries management	**M**				***H***		***H***	
Land use		**M**				**M**	*U*	
Nuisance species introduction and management			***H***			***H***		
Onsite vegetation management		***H***			***H***		**M**	
Onsite water management	**L**					**M**		
Water storage-delivery system design and operations							**M**	

CAUSAL RELATIONSHIPS WITH HIGH UNDERSTANDING

Many causal relationships proposed in the CEM (see above, this chapter, and chapter 6) are rated as having high understanding. The CEM proposes these relationships based on established ecological principles, knowledge of frog biology and ecology in general, published information on the regulated LCR ecosystem overall, and detailed studies of LLFR. The latter detailed studies include investigations by Rosen et al. (2013) and others (Parker 2006; Swann and Wallace 2010; Wallace et al. 2010) in southeastern Arizona and by the AZGFD in the LCR, Bill Williams, Agua Fria, and Verde River valleys (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014, 2016; Leavitt et al. 2017); Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b).

The CEM identifies 11 causal relationships between individual controlling factors. These relationships apply to all three LLFR life stages. The CEM rates 7 of these 11 causal relationships as having high understanding, based on numerous publications concerning resource management along the LCR valley, as discussed in chapters 4 and 5. These seven involve the following:

- Bi-directional causal relationships between fisheries management and nuisance species introduction and management, between onsite vegetation management and fire management, and between onsite vegetation management and nuisance species introduction and management.

- Uni-directional causal relationships between fisheries management and channel and off-channel engineering, between fisheries management and onsite water management, between onsite water management and fire management, and between water storage-delivery system design and operations and onsite water management.

The CEM identifies 36 causal relationships between controlling factors and habitat elements, which also apply to all 3 LLFR life stages. The CEM rates 14 of these 36 causal relationships as having high understanding, based on general ecological principles and publications concerning resource conditions and management along the LCR valley, as discussed also in chapters 4 and 5. These 14 involve exclusively uni-directional causal relationships between the following:

- Channel and off-channel engineering and (a) hydrologic regime and (b) substrate

- Conservation monitoring and research programs and (a) fish and herpetofauna and (b) monitoring, capture, and handling

- Fisheries management and fish and herpetofauna

- Nuisance species introduction and management and woody vegetation

- Onsite vegetation management and airborne contaminants

- Onsite water management and (a) hydrologic regime, (b) water chemistry, and (c) water temperature

- Water storage-delivery system design and operations and (a) hydrologic regime, (b) substrate, (c) water chemistry, and (d) water temperature

The CEM identifies much less certainty in knowledge concerning possible causal interactions among habitat elements, between habitat elements and critical biological activities and processes, among critical biological activities and processes, between critical biological activities and processes and life-stage outcomes, or among life-stage outcomes. Chapters 3–6 provide detailed explanations. Specifically:

- The CEM identifies 36 causal relationships among habitat elements, all of which apply across all 3 LLFR life stages, but identifies only 3 of these as having high understanding. These three are the effects of the hydrologic regime on water chemistry and water temperature, and the effects of water temperature on water chemistry.

- The CEM identifies 13 causal relationships between habitat elements and critical biological activities and processes for the egg life stage, and it identifies 23 for the larval-juvenile life stage, none of which warranted a rating of high for understanding for either life stage.

- The CEM identifies 33 causal relationships between habitat elements and critical biological activities and processes for the adult life stage, but it identifies only 8 of these as having high understanding. These eight relationships for the adult life stage are: uni-directional effects of herbaceous vegetation on (a) mating and ovipositing and (b) occupancy and inter-site movement; uni-directional effects of the hydrologic regime on (a) mechanical stress and (b) resting/hiding behavior; uni-directional effects of infectious agents on disease; uni-directional effects of woody vegetation on (a) mating and ovipositing and (b) occupancy and inter-site movement; and a bi-directional relationship between monitoring, capture, and handing and resting/hiding behavior.

- The CEM for the egg life stage identifies 16 causal relationships among critical biological activities and processes, between critical biological activities and processes and life-stage outcomes, and between the 2 life-stage outcomes for this life stage, but it does not identify any that warrant a rating of high for understanding. The CEM similarly finds 25 such causal relationships for the larval-juvenile life stage and 43 such relationships for the adult life stage, but it does not identify any that warrant a rating of high for understanding for either life stage.

POTENTIALLY INFLUENTIAL CAUSAL RELATIONSHIPS WITH LOW UNDERSTANDING AND/OR UNKNOWN MAGNITUDE

Many causal relationships proposed in the CEM (see above, this chapter, and chapter 6) are rated as having low understanding. The CEM proposes these relationships based on established ecological principles, knowledge of frog biology and ecology in general, and suggestions in the literature on LLFR or on closely related species. However, few or no studies provide actual evidence concerning these relationships specifically for LLFR or any closely related species or concerning relevant habitat element conditions and dynamics in the greater LCR ecosystem. In many instances, the gaps in knowledge are so large that the CEM assigns a rating of unknown for link magnitude as well. The CEM includes links with unknown magnitude, based on established ecological principles and knowledge of frog biology and ecology in general, for which there is no documentation specifically for LLFR or any closely related species (e.g., for any other leopard frog). For example, the LCR ecosystem contains numerous insectivorous birds, and basic ecological principles suggest that some of these birds consequently may compete with LLFR adults for food items; however, the literature does not contain sufficient information on food item selection by LLFR adults to allow any assessment of the likely magnitude of such competition. Links rated as having low understanding appear in the LLFR life-stage diagrams in chapter 6 (figures 3–5) as red arrows; links with unknown magnitude appear in these diagrams as extremely thin red arrows.

Tables 13–15 summarize information on links rated as low for understanding and either high or unknown for magnitude. These tables thus identify potentially significant gaps in knowledge concerning LLFR in general or in the LCR ecosystem in particular. Table 13 looks specifically at direct causal relationships among life-stage outcomes. Table 14 looks at direct causal relationships between critical biological activities and processes and life-stage outcomes. Table 15 looks at direct causal relationships between habitat elements and critical biological activities and processes. The key for tables 13–15 is the same as for tables 8–12, above.

Table 13 indicates that several aspects of LLFR biology are poorly understood. The CEM identifies only one of the links with low understanding as warranting a rating of high for magnitude, specifically the effect of adult survival on adult fertility. The rating for magnitude reflects a basic biological principle. Otherwise, the CEM identifies possible links between growth and survival for all three LLFR life stages, growth and fertility for adults, and survival and gene flow for adults, for which the literature does not provide sufficient information to warrant any rating for link magnitude for LLFR. For example, the literature on frogs, in general, indicates that larger adults may have higher fertility, but none of the literature on LLFR or any closely related frogs addresses the topic.

Table 13.—Low-understanding, high- or unknown-magnitude direct effects of life-stage outcomes on each other across all LLFR life stages
(See table 8 for key.)

Affected life-stage outcome ➔ / **Causal life-stage outcome 🡻**	**Egg survival**	**Larval-juvenile survival**	**Adult fertility**	**Adult growth**	**Adult survival**	**Gene flow**
Egg growth	*U*					
Larval-juvenile growth		*U*				
Adult growth			*U*		*U*	
Adult survival			***H***	*U*		*U*

Table 14 indicates that several additional aspects of LLFR biology are poorly understood – in this case, the effects of critical biological activities and processes on life-stage outcomes. Among 24 direct links between critical biological activities and processes and life-stage outcomes with low understanding, the CEM identifies only 8 as warranting a rating of high for magnitude. Six of these eight concern the effects of foraging on growth and survival, and the effects of fertility; and one concerns the effects of occupancy and inter-site movement on gene flow. The rating for magnitude for these 8 links reflects a basic principle of frog biology. At the same time, the CEM identifies possible links between predation on survival; one concerns the effects of mating and ovipositing on chemical stress, disease, hydration stress, mechanical stress, and resting/hiding behaviors among LLFR, for which the literature does not provide sufficient information to warrant any rating for link magnitude for LLFR. Similarly, the CEM proposes

Table 14.—Low-understanding, high- or unknown-magnitude direct effects of critical biological activities and processes on life-stage outcomes across all LLFR life stages (See table 8 for key.)

Affected life-stage outcome ➔ / Causal critical biological activity or process 🡻	Egg growth	Egg survival	Larval-juvenile growth	Larval-juvenile survival	Adult fertility	Adult growth	Adult survival	Gene flow
Chemical stress	*U*		*U*			*U*		
Disease	*U*				*U*			
Foraging			***H***	***H***		***H***		
Hydration stress	*U*		*U*		*U*	*U*		
Mating and ovipositing					***H***			
Mechanical stress					*U*			
Occupancy and inter-site movement						*U*	*U*	***H***
Predation		***H***		***H***			***H***	
Resting/hiding			*U*	*U*		*U*	*U*	

effects of LLFR site occupancy and inter-site movement patterns on adult growth and survival, for which the literature does not provide sufficient information to warrant any rating for link magnitude.

Table 15, in turn, indicates that several aspects of LLFR ecology are poorly understood – in this case, the effects of habitat elements on critical biological activities and processes in one or more life stages. Table 15 indicates that the CEM proposes the following:

- The compositions and densities of the bird and mammal assemblages likely affect the rate of predation faced by all three LLFR life stages with high magnitude, but the literature provides little information on the subject other than to identify these as likely relationships.

- Drainage network connectivity likely affects the rates and patterns of LLFR site occupancy and inter-site movement with high magnitude, but the literature provides little information on the subject other than to identify this as a likely relationship.

Table 15.—Low-understanding, high- or unknown-magnitude direct effects of habitat elements on critical biological activities and processes across the three LLFR life stages
(See table 8 for key.)

Affected critical biological activity or process ➔ **Causal habitat element 🡻**	**Competition**	**Disease**	**Foraging**	**Hydration stress**	**Mechanical stress**	**Occupancy and inter-site movement**	**Predation**	**Resting/hiding**	**Thermal stress**
Birds and mammals	- - *U*						***H*** ***H*** ***H***		
Drainage network connectivity						- - ***H***			
Fire regime									*U* *U* *U*
Fish and herpetofauna	- *U* -		- *U* *U*				***H*** - ***H***		
Herbaceous vegetation								- ***H*** -	
Infectious agents		***H*** - -							
Macroinvertebrates	- ***H*** -		- - ***H***				***H*** ***H*** -		
Monitoring, capture, handling				*U* *U* *U*	*U* *U* *U*			- *U* -	
Periphyton and particulate organic matter (POM)			- ***H*** -						
Woody vegetation								- ***H*** -	

- The compositions and densities of the fish and herpetofaunal assemblages likely affect the rate of predation faced by LLFR eggs and adults with high magnitude, but the literature provides little information on the subject other than to identify these as likely relationships. Knowledge is more certain concerning fish and herpetofaunal predation on LLFR larvae and juveniles.

- The compositions and densities of the herbaceous and woody vegetation assemblages likely affect larval-juvenile resting/hiding behaviors with high magnitude, but the literature provides little information on the subject other than to identify this as a likely relationship. Knowledge is more certain concerning the effects of these assemblages on LLFR adults and their selection of locations for ovipositing.

- The types and abundances of infectious agents in the system likely affect disease rates in LLFR eggs with high magnitude, but the literature provides little information on the subject other than to identify this as a likely relationship. Knowledge is more certain concerning this relationship for LLFR larvae-juveniles and adults.

- The composition and density of the macroinvertebrate assemblage, particularly the assemblage of aquatic macroinvertebrates, likely affect the rate of competition faced by LLFR larvae-juveniles, foraging success among LLFR adults, and the rates of predation experienced by LLFR eggs and larvae-juveniles, all with high magnitudes. However, the literature provides little information on these proposed links other than to identify them as likely relationships.

- The composition and density of the periphyton and POM assemblages likely affect foraging behavior and rates of success among LLFR larvae-juveniles with high magnitude, but the literature provides little information on the subject other than to identify this as a likely relationship.

Table 15 also shows that the CEM identifies several possible links for which the literature does not provide sufficient information to warrant any rating for link magnitude, as follows:

- The possible effects of birds and mammals on the rate of competition faced by LLFR adults.

- The possible effects of the fire regime on thermal stress in all three LLFR life stages.

- The possible effects of fish and herpetofauna on the rate of competition faced by LLFR larvae-juveniles and on foraging behaviors and success rates among LLFR larvae-juveniles and adults.

- The possible effects of monitoring, capture, and handling on hydration stress and mechanical stress among LLFR in all three life stages and on resting/hiding behaviors among LLFR larvae-juveniles.

Chapter 8 – Discussion and Conclusions

The LLFR conceptual ecological model has several notable features. First, the assessment of the causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes indicates the following strong (high-magnitude) causal relationships:

- Seven controlling factors have direct, high-magnitude effects on one or more habitat elements. These are, in alphabetical order: conservation monitoring and research programs; fire management; fisheries management; land use; nuisance species introduction and management; onsite water management; and water storage-delivery system design and operations.

- Twelve habitat elements have direct, high-magnitude effects on 1 or more critical biological activities and processes. These are, in alphabetical order: birds and mammals; drainage network connectivity; fish and herpetofauna; herbaceous vegetation; hydrologic regime; infectious agents; macroinvertebrates; monitoring, capture, handling; periphyton and POM; substrate; water temperature; and woody vegetation.

- Nine habitat elements have direct, high-magnitude effects on one or more other habitat elements, and thereby have (or additionally have) strong indirect effects on one or more critical biological activities or processes in one or more life stages. These are, in alphabetical order: birds and mammals; fire regime; fish and herpetofauna; herbaceous vegetation; hydrologic regime; macroinvertebrates; substrate; water temperature; and woody vegetation. Eight habitat elements—birds and mammals; fish and herpetofauna; herbaceous vegetation; hydrologic regime; macroinvertebrates; substrate; water temperature; and woody vegetation—thus have high-magnitude *direct and indirect* effects on one or more critical biological activities or processes among the three LLFR life stages.

- Four critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes among the three LLFR life stages. These are, in alphabetical order: foraging; mating and ovipositing; occupancy and inter-site movement; and predation. Foraging specifically has direct, high-magnitude effects on larval-juvenile growth, larval-juvenile survival, and adult growth. Mating and ovipositing has direct, high-magnitude effects on adult fertility. LLFR site occupancy and inter-site movement has direct, high-magnitude effects on gene flow. Predation has direct, high-magnitude effects on survival in all three life stages.

- Two critical biological activities or processes have direct, high-magnitude effects on one or more other critical biological activities or processes and thereby have (or additionally have) strong indirect effects on one or more life-stage outcomes across the three LLFR life stages. These two critical biological activities or processes are competition and predation. Both competition and predation have direct, high-magnitude effects on LLFR occupancy and inter-site movement.

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.

Second, the assessment of causal relationships identifies a large number with low understanding. These include several links for which the available information indicates a likely high-magnitude relationship but also links for which the available information is too scant to rate magnitude at all. This chapter provides a detailed list of links with high or unknown magnitude, which may comprise areas of significant uncertainty for species management. The CEM includes links with unknown magnitude based on established ecological principles and knowledge of particular features of frog biology and ecology, in general, for which there is no documentation specifically for LLFR or any closely related species.

- The CEM identifies seven potential links among life-stage outcomes across the three LLFR life stages, all rated low for understanding. Of these seven, all but one is rated as unknown for link magnitude. The one exception is the relationship between adult survival on adult fertility, which warrants a rating of high for magnitude based on basic biological principles.

- The CEM identifies 24 potential links between critical biological activities and processes and life-stage outcomes across the 3 LLFR life stages that are rated low for understanding and either high or unknown for magnitude. As shown in table 14, 16 of these 24 links are rated as unknown for link magnitude. For example, the CEM recognizes that chemical stress can impair growth in all three life stages, based on basic biological principles, but also recognizes that the literature provides no clues on whether or to what magnitude this relationship may affect LLFR in any life stage.

- The CEM identifies 27 potential causal links between habitat elements and critical biological activities and processes across the 3 LLFR life stages, for which the available information suggested a rating of low for understanding and a rating of either high or unknown for magnitude. As shown in table 15, the CEM specifically rates link magnitude for 14 of these 27 links as unknown. These 14 include proposed effects of birds and mammals and fish and herpetofauna on competition in the adult life stage; proposed effects of the fire regime on thermal stress in all three life stages; proposed effects on fish and herpetofauna on foraging by LLFR larvae and adults; proposed effects of monitoring, capture, and handling on both hydration stress and mechanical stress in all three life stages; and proposed effects of monitoring, capture, and handling on larval and juvenile resting/hiding behavior.

Finally, the CEM does identify several potentially important causal relationships with high magnitude *and high or medium understanding*. These ratings of medium or high for link understanding reflect cumulative knowledge from several detailed studies of LLFR and their habitat, including the several studies by the AZGFD in the LCR, Bill Williams, Agua Fria, and Verde River valleys. These well and moderately well-understood, high-magnitude relationship include:

- Proposed high-magnitude links with medium understanding for the larval-juvenile life stage, concerning the effects of infectious agents on disease and the effects of fish and herpetofauna on predation.

- Proposed high-magnitude links with medium understanding for the adult life stage, concerning the effects of water temperature on mating and ovipositing, the effects of substrate texture and stability on adult resting/hiding behavior, and the effects of the hydrologic regime on site occupancy and inter-site movement.

- Proposed high-magnitude links with high understanding for the adult life stage, concerning the effects of woody vegetation on mating and ovipositing, resting/hiding, and site occupancy and inter-site movement; the effects of herbaceous vegetation on mating and ovipositing, and site occupancy and inter-site movement; and the effects of monitoring, capture, and handling on LLFR adult resting/hiding behavior, and vice versa.

- Proposed high-magnitude links with medium understanding for the adult life stage, concerning the effects of competition and predation on site occupancy and inter-site movement.

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ATTACHMENT 1

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

OVERVIEW OF METHODOLOGY

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

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

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

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

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

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

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

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

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

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

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

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

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.

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. The present CEM methodology includes methods for assessing causal relationships (links) along four dimensions (attributes) adapted from the ERP methodology (DiGennaro et al. 2012):

(1) The character and direction of the effect

(2) The magnitude of the effect

(3) The predictability (consistency) of the effect

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

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

Second, the 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.

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

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

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

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

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

Conceptual Ecological Model Documentation

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

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

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

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

Link Attribute Ratings, Spreadsheet Fields, and Diagram Conventions

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

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

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

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

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

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

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

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

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

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

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

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

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

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

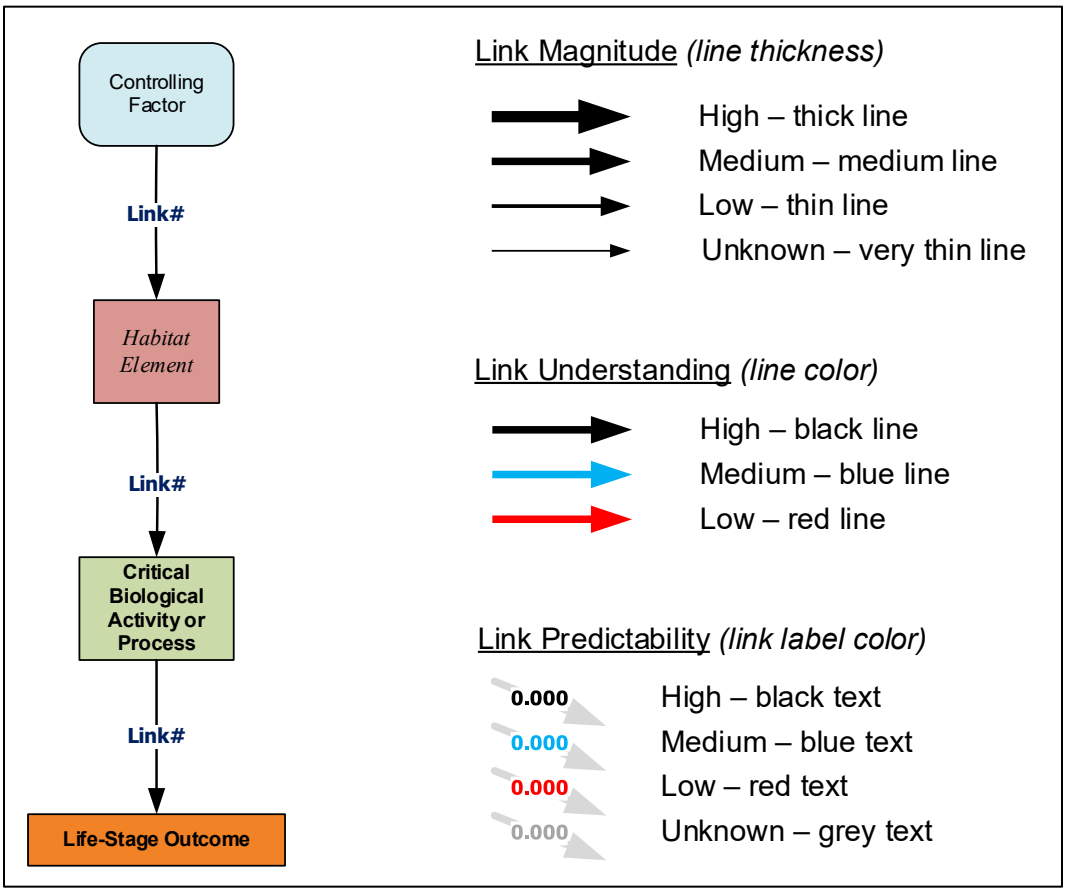

Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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