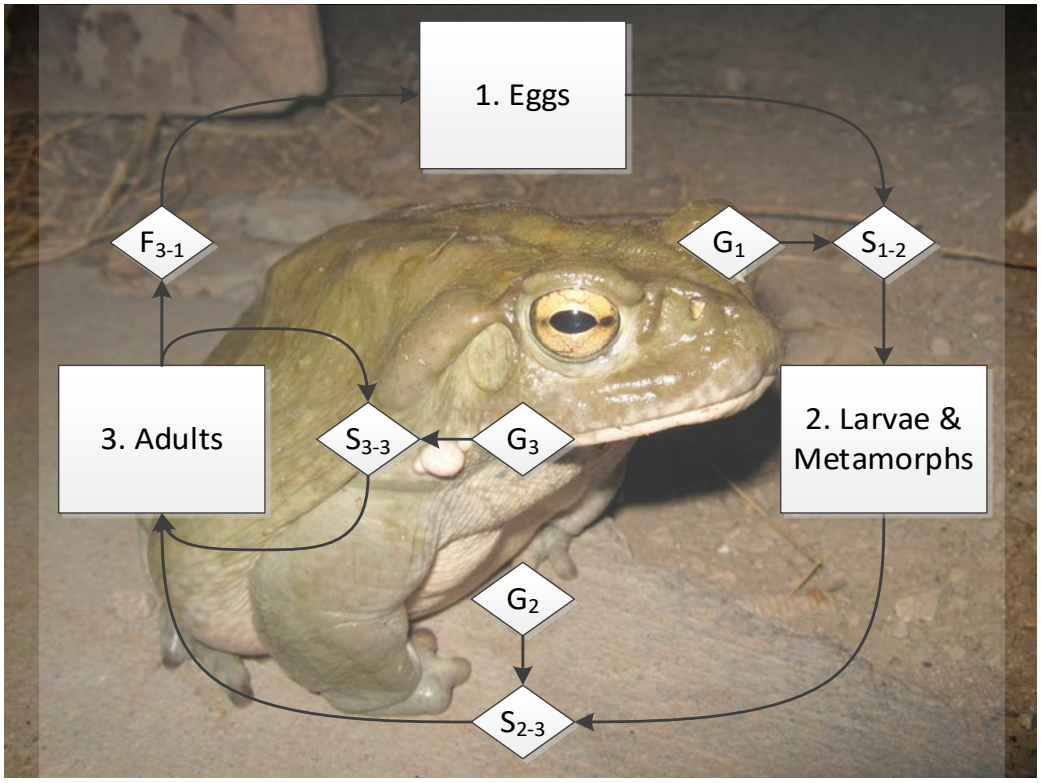
Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Colorado River Toad (*Bufo = Incilius alvarius*) (CRTO) Basic Conceptual Ecological Model for the Lower Colorado River



September 2020

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Lower Colorado River Multi-Species Conservation Program

Colorado River Toad (*Bufo* = *Incilius alvarius*) (CRTO) Basic Conceptual Ecological Model for the Lower Colorado River

Prepared by:

David P. Braun, Ph.D., Elizabeth A. Johnson, and Robert Unnasch, Ph.D.

Sound Science, LLC

Lower Colorado River
Multi-Species Conservation Program
Bureau of Reclamation
Lower Colorado Basin
Boulder City, Nevada
http://www.lcrmscp.gov

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ACRONYMS AND ABBREVIATIONS

AZGFD	Arizona Game and Fish Department
Bd	*Batrachochytrium dendrobatidis*
CCDI	cost-corrected detection index
CEM	conceptual ecological model
CI	confidence interval
cm	centimeter(s)
CRAB	Colorado River Aquatic Biology
CRTO	Colorado River toad (*Bufo* = *Incilius alvarius*)
CRTR	Colorado River Terrestrial and Riparian (meeting)
d	day(s)
DAR	digital automated recorder
DNA	deoxyribonucleic acid
eDNA	environmental deoxyribonucleic acid
EPA	U.S. Environmental Protection Agency
FTA	funnel trap array
Goldwater Range-East	Barry M. Goldwater Air Force Range-East (U.S. Air Force)
ha	hectare(s)
HCP	Habitat Conservation Plan
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
mm	millimeter(s)
mo	month(s)
pH	the acidity or alkalinity of a solution
POM	particulate organic matter
Reclamation	Bureau of Reclamation
SE	standard error
SVL	snout-vent length

USFWS	U.S. Fish and Wildlife Service
UV-B radiation	ultraviolet-B radiation
VES	visual encounter survey
VES C/R	visual encounter survey with an audio broadcast call/response component
yr	year(s)

Symbols

°C	temperature in degrees Celsius (*aka* Centigrade)
>	greater than
≥	greater than or equal to
<	less than
%	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. 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 (see 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 Colorado River toad (*Bufo = Incilius alvarius*) (CRTO), also known as the Sonoran Desert toad. The genus *Incilius* comprises a large group of toad species known as Central American bufonids (Mendelson, III et al. 2011; Thomson et al. 2016). Most members of this genus live in Mexico, Central America, and northernmost South America.

The CRTO is an evaluation species for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Bureau of Reclamation (Reclamation). The LCR MSCP planning area includes the Colorado River from Separation Canyon (lower Grand Canyon) to the U.S.-Mexico border and its adjacent floodplain, the full pool elevations of its three main reservoirs (Lakes Mead, Mojave, and Havasu), and the lower ends of the Virgin and Bill Williams Rivers inundated by these three main reservoirs (LCR MSCP 2004).

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

This CEM addresses the present CRTO population and its distribution within the greater lower Colorado River (LCR) ecosystem, including the LCR MSCP planning area. The greater LCR ecosystem includes the LCR floodplain and adjacent uplands, and the floodplains and adjacent uplands of tributaries to the main stem (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a). CRTO currently are known only to occur in scattered locations along the east side of the greater LCR ecosystem in La Paz and Yuma Counties, Arizona, including in the Bill Williams River watershed below Alamo Dam. These occurrences mark the westward limits of its current distribution, which in the United States also includes land below approximately 1600-meter (m) elevation eastward across the rest of southern Arizona into the southwest corner of New Mexico, and which in Mexico includes the northeast corner of Baja California, the western two-thirds of Sonora, and northwestern Sinaloa (Arizona Game and Fish Department [AZGFD] 2019; Hammerson and Santos-Barrera 2004). Historically, CRTO occurred along the Lower Colorado River Valley from the Colorado River Delta northward to the area of Blythe, California, and Ehrenberg, Arizona, and possibly as far north as Fort Mohave, Arizona, and as far

west as the Imperial Valley, California (LCR MSCP 2016; Nafis 2019; Thomson et al. 2016). However, some reports question whether the Imperial Valley was a natural part of their historic range or an area into which CRTO expanded following the development of irrigation agriculture there (Thomson et al. 2016).

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 CRTO. These research questions and knowledge gaps may or may not be relevant to the goals of the LCR MSCP; as such, they are not to be considered guidance for Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

CONCEPTUAL ECOLOGICAL MODELS

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

The CEM methodology distinguishes the major life stages or events through which the individuals of a species must pass to complete a full life cycle. It then identifies the factors that shape the likelihood that individuals in each life stage will survive to the next stage in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

Specifically, the CEM has five core components:

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

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

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

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

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

The CEM identifies the causal relationships among these components for each life stage. A causal relationship exists when a change in one condition or property of a system results in a change in some other condition or property. A change in the first condition is said to cause a change in the second condition. The CEM method applied here assesses four variables for each causal relationship:

1. The character and direction of the effect, rated as either uni- or bi-directional

2. The magnitude of the effect, rated as high, medium, low, or unknown

3. The predictability (consistency) of the effect, rated as high, medium, low, or unknown

4. The certainty of a present scientific understanding of the effect, rated as high, medium, or low

CEM diagrams and a linked spreadsheet tool document all information on the model components and their causal relationships, including the reasoning for their ratings for effect direction, magnitude, predictability, and understanding. 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 basic sources of information for this CEM consist of species accounts by the AmphibiaWeb (2019), which updates information from Fouquette, Jr. et al. (2005); LCR MSCP (2016); Nafis (2019); NatureServe (2019); and Thomson et al. (2016). These publications summarize and cite numerous earlier studies. This CEM also rests on reports from Kiesow 2015 (see also Griffis-Kyle et al. 2019; Kiesow and Griffis-Kyle 2017) on breeding habitat and activity among CRTO and two other desert toads in 2010 and 2012 in the Barry M. Goldwater Air Force Range-East (Goldwater Range-East), east of Yuma, Arizona; and reports prepared by the AZGFD for the LCR MSCP on the current distribution, breeding habitat requirements, and most effective monitoring methods for CRTO in the LCR and Bill Williams, Agua Fria, and Verde River valleys, Arizona, based on field investigations in 2011–16 (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a, 2016; Leavitt et al. 2017; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b). The AZGFD studies addressed both CRTO and the lowland leopard frog (*Rana* = *Lithobates yavapaiensis*), a covered species for the LCR MSCP. This CEM shares several features with the CEM prepared for the latter species (Braun et al. 2020).

This CEM also incorporates information concerning anuran biology in general and the environmental settings in which CRTO can occur; the expert knowledge of LCR MSCP biologists; and information presented at the annual Colorado River Terrestrial and Riparian (CRTR) and Colorado River Aquatic Biology (CRAB) meetings in 2011–17[2] (Cotten 2012, 2013a, 2013b; Cotten and Leavitt 2014b;

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

Cotten et al. 2015; Frary 2011; Miller 2016; O'Donnell and Leavitt 2017c). However, the purpose of this document is not to provide a literature review; rather, its purpose is to integrate current knowledge into a CEM so it can be used for adaptive management.

The CRTO 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 life stage: egg growth, egg survival
- Larvae and metamorphs life stage: larval-metamorph growth, larval-metamorph survival
- Adults life stage: adult growth, adult survival, adult fertility

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 on the extensive literature on toad biology indicating that the rates of growth in all three life stages and attained sizes in the larval-metamorph and adults life stages affect survival rates, adult mating success, and fertility.

The CRTO conceptual ecological model identifies 10 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 10 critical biological activities and processes are as follows, in alphabetical order: aggregation/dispersion, breeding, chemical stress, competition, disease, foraging, mechanical stress, predation, resting/hiding, and thermal stress.

The CRTO conceptual ecological model distinguishes 10 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 10 habitat elements are as follows, in alphabetical order: arthropod community; chemical contaminants; fire regime; infectious agents; monitoring, capture, handling; periphyton & particulate organic matter; temperature; vegetation assemblage; vertebrate community; and water availability.

Finally, the CRTO conceptual ecological model distinguishes seven controlling factors that affect the distribution, quality, composition, abundance, and other features of one or more of these habitat elements. Because environmental conditions in the greater LCR ecosystem are highly managed, the controlling factors almost exclusively concern human activities. Chapter 5 defines and discusses these controlling factors in detail. The seven controlling factors are as follows, in alphabetical order: conservation monitoring & research programs, fire

management, habitat development & management, land use, nuisance species introduction & management, on-site water management, and water storage-delivery system design & operation.

RESULTS

This CEM identifies several direct, strong (high-magnitude) causal relationships among these controlling factors, habitat elements, critical biological activities and processes, and life-stages (with varying levels of link understanding). These are not necessarily the only causal relationships that strongly affect habitat elements, critical biological activities or processes, or life-stage outcomes in the greater LCR ecosystem. However, the relationships identified as high-magnitude (or medium- or low-magnitude) links are merely those for which it was possible to develop a rating for link magnitude based on the available evidence. Links for which there was not sufficient information to support a rating of link magnitude received a rating of "unknown" for magnitude. As knowledge of CRTO grows, at least some of these latter links may eventually prove to be high-magnitude relationships.

This CEM proposes that four controlling factors have direct, high-magnitude effects on one or more habitat elements across all three life stages. It assigns ratings of low understanding to only a handful of these relationships, each affecting all three life stages. Chapters 4 and 5 discuss the sources of uncertainty for these causal relationships between controlling factors and habitat elements. The four dominant controlling factors are, in alphabetical order:

- Conservation monitoring &research programs, which directly and strongly affect monitoring, capture, handling
- Fire management, which directly and strongly affects the fire regime
- Land use, which directly and strongly affects the arthropod and vertebrate communities
- Nuisance species introduction & management, which directly and strongly affects the arthropod community, vegetation assemblage, and vertebrate community

This CEM proposes that six habitat elements have direct, high-magnitude effects on one or more critical biological activities or processes in one or more life stages. It assigns ratings of low understanding to three of these relationships, each affecting either one or two life stages. Chapters 3 and 4 discuss the sources of uncertainty for these causal relationships between habitat elements and critical

biological activities and processes. The habitat elements with high-magnitude effects on critical biological activities or processes are, in alphabetical order:

- The arthropod community, which directly and strongly affects foraging by CRTO larvae and adults and predation on CRTO larvae and metamorphs
- Periphyton & POM, which directly and strongly affects foraging by CRTO larvae
- Temperature, which directly and strongly affects breeding in CRTO adults
- The vegetation assemblage, which directly and strongly affects aggregation/dispersion and breeding in CRTO adults
- The vertebrate community, which directly and strongly affects foraging by CRTO adults and predation on CRTO larvae, metamorphs, and adults
- Water availability, which directly and strongly affects CRTO adult breeding

This CEM proposes that one critical biological activity or process, CRTO adult breeding, conversely affects one habitat element, monitoring, capture, handling, with high magnitude. CRTO may not call during breeding, and even when they do, their calls are quiet. These aspects of CRTO behavior limit the effectiveness of visual encounter surveys with an audio broadcast call/response component (VES C/Rs) and digital automated recorder (DAR) methods for detecting breeding CRTO.

This CEM proposes that seven habitat elements have direct, high-magnitude effects on one or more other habitat elements and thereby have strong indirect effects on one or more critical biological activities or processes in one or more life stages. It assigns ratings of low understanding to all of the high-magnitude reciprocal cause-effect relationships between habitat elements. Chapter 4 discusses the sources of uncertainty for these causal relationships. The habitat elements with high-magnitude effects on other, dominant habitat elements are, in alphabetical order:

- The fire regime, which directly and strongly affects the vegetation assemblage and *vice versa*
- Periphyton & POM, which directly and strongly affects the arthropod community

- Temperature, which directly and strongly affects chemical contamination

- The vegetation assemblage, which directly and strongly affects the arthropod and vertebrate communities and *vice versa*

- The vertebrate community, which directly and strongly affects the arthropod community and *vice versa*, specifically in CRTO breeding habitat

- Water availability, which directly and strongly affects the vegetation assemblage and vertebrate community

This CEM proposes that two critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes across the three CRTO life stages. It assigns ratings of low understanding to all high-magnitude effects of critical biological activities or processes on CRTO life-stage outcomes. Chapter 3 discusses the sources of uncertainty for these causal relationships. The critical biological activities or processes with high-magnitude effects on life-stage outcomes are as follows:

- Breeding in the CRTO adults life stage directly and strongly affects adult fertility and adult survival. The effect on adult survival is bi-directional because CRTO adults may be particularly vulnerable to predation while breeding, and predator attacks during CRTO breeding will disrupt the mating process.

- CRTO adult and larval foraging both directly and strongly affect growth during these life stages, and reciprocally, greater growth during these life stages increases foraging success.

This CEM proposes that one critical biological activity or process has direct, high-magnitude effects on one other critical biological activity or process for one life stage. Specifically, CRTO adult resting/hiding behavior affects their vulnerability to thermal stress. This CEM assigns a rating of high to understanding of this relationship. Chapter 3 discusses this link further.

This CEM proposes a large number of causal relationships for which understanding is low, including several links for which, as noted above, knowledge is too limited to support any rating of link magnitude at all. It includes links with low understanding based on basic principles of biology for anurans, desert toads, or Central American bufonids in general. Of the 244 links included, across all life stages combined, the CEM rates162 (66%) as having low understanding. Of those links with low understanding, the CEM rates 75 (46%) as unknown for magnitude, 21 (13%) as having low magnitude, 26 (16%) as having medium magnitude, and 40 (25%) as having high magnitude. These

results indicate a lack of species-specific evidence on many aspects of CRTO ecology, biology, or behavior that could help guide species or habitat management. As knowledge about the species expands, the ratings of link magnitude may change, including changing from unknown to a more definite rating value.

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for the Colorado River toad, also known as the Sonoran Desert toad, *Bufo = Incilius alvarius*[1] (CRTO). The CRTO is an evaluation species for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Bureau of Reclamation (Reclamation). The LCR MSCP planning area includes the Colorado River from Separation Canyon (lower Grand Canyon) to the U.S.-Mexico border and its adjacent floodplain, the full pool elevations of its three main reservoirs (Lakes Mead, Mojave, and Havasu), and the lower ends of the Virgin and Bill Williams Rivers inundated by these three main reservoirs (LCR MSCP 2004).

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

This CEM addresses the present CRTO population and its distribution within the greater lower Colorado River (LCR) ecosystem, including the LCR MSCP planning area. The greater LCR ecosystem includes the LCR floodplain and adjacent uplands, and the floodplains and adjacent uplands of tributaries to the main stem (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a). CRTO currently are known to occur only in scattered locations along the east side of the greater LCR ecosystem in La Paz and Yuma Counties, Arizona, including in the Bill Williams River watershed below Alamo Dam. These occurrences mark the westward limits of their current distribution, which in the United States also includes land below approximately 1600-meter (m) elevation eastward across the rest of southern Arizona into the southwest corner of New Mexico, and which in Mexico includes the northeast corner of Baja California, the western two-thirds of Sonora, and northwestern Sinaloa (Hammerson and Santos-Barrera 2004; Arizona Game and Fish Department [AZGFD] 2019). Historically, CRTO occurred along the Lower Colorado River Valley from the Colorado River Delta northward to the area of Blythe, California, and Ehrenberg, Arizona, and possibly as far north as Fort Mohave, Arizona, and as far west as the Imperial Valley, California (LCR MSCP 2016; Nafis 2019; Thomson et al. 2016). However, some reports question whether the Imperial

[1] AZGFD (2019), Frost (2019), and NatureServe (2019) use the generic identifier, *Incilius*, but Thomson et al. (2016) consider this taxonomy controversial and prefer *Bufo*.

Valley was a natural part of their historic range or an area into which they expanded following the development of irrigation agriculture there (Thomson et al. 2016).

The basic sources of information for this CEM consist of species accounts by AmphibiaWeb (2019), which updates information from Fouquette, Jr. et al. (2005); the LCR MSCP (2016); Nafis (2019); NatureServe (2019); and Thomson et al. (2016). These publications summarize and cite numerous earlier studies. This CEM also rests on reports from Kiesow 2015 (see also Griffis-Kyle et al. 2019; Kiesow and Griffis-Kyle 2017) on breeding habitat and activity among CRTO and two other desert toads in 2010 and 2012 in the U.S. Air Force's Barry M. Goldwater Range-East (Goldwater Range-East), east of Yuma, Arizona; and reports prepared by the AZGFD for the LCR MSCP on the current distribution, breeding habitat requirements, and most effective monitoring methods for CRTO in the LCR and Bill Williams, Agua Fria, and Verde River valleys, Arizona, based on field investigations in 2011–16 (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a, 2016; Leavitt et al. 2017; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b). The AZGFD studies addressed both CRTO and the lowland leopard frog (*Rana = Lithobates yavapaiensis*), a covered species for the LCR MSCP. This CEM shares several features with the CEM prepared for the latter species (Braun et al. 2020).

This CEM also incorporates information concerning anuran biology in general and the environmental settings in which CRTO can occur; the expert knowledge of LCR MSCP biologists; and information presented at the annual Colorado River Terrestrial and Riparian (CRTR) and Colorado River Aquatic Biology (CRAB) meetings in 2011–17[2] (Cotten 2012, 2013a, 2013b; Cotten and Leavitt 2014b; Cotten et al. 2015; Frary 2011; Miller 2016; O'Donnell and Leavitt 2017c). However, the purpose of this document is = not to provide a literature review; rather, its purpose is to integrate current knowledge into a CEM so it can be used for adaptive management.

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

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

COLORADO RIVER TOAD REPRODUCTIVE ECOLOGY

The CRTO is a member of a large group of species known as Central American bufonids, comprising the genus *Incilius* (Mendelson, III et al. 2011; Thomson et al. 2016). Most members of this genus live in Mexico, Central America, and northernmost South America. Only a few, including CRTO, have ranges that extend into the United States, mostly into the Sonoran and Chihuahuan Desert ecoregions. Mendelson, III et al. (2011) identify a "…reproductive strategy of placing eggs in temporary or permanent puddles and ponds during the rainy season" as "…the plesiomorphic [ancestral] condition for *Incilius*." Mendelson, III et al. (2011) also identify CRTO, in particular, as a basal species in the lineage (i.e., a species that retains a large number of such ancestral characteristics). The same authors also note that the species in this lineage as a whole are "…relatively tolerant of human habitat disruption, and individuals of almost all species may be found in a variety of disturbed habitats including towns, agricultural lands, roadside ditches, and every variety of secondary growth."

The basic species accounts for CRTO (AmphibiaWeb 2019, which updates information from Fouquette, Jr. et al. 2005; LCR MSCP 2016; Nafis 2019; NatureServe 2019; Thomson et al. 2016) document that sexually mature CRTO gather seasonally at relatively shallow, still or low-velocity water bodies to mate. These water bodies may be either ephemeral or permanent natural pools or stream backwaters, or artificial water bodies such as cattle (Bovidae) watering ponds (*aka* "cattle tanks") or slow-flowing irrigation canals or ditches. However, CRTO gather in these locations only for 1 or 2 nights a year, usually following substantial rainfall—greater than 25 millimeters (mm) in a single 24-hour period (Sullivan and Fernandez 1999)—during the so-called "monsoon" thunderstorm season that characterizes this part of the Southwestern United States from late May into August. If the rainfall is too heavy (e.g., greater than 75 mm over a 24-hour period) and causes local flooding, the toads may wait 2 or 3 days for the water to subside into still pools before they gather (Fouquette, Jr. et al. 2005). CRTO also may gather at potential breeding sites before the onset of rainfall (Fouquette, Jr. 1970) and may continue calling to attract mates for as long as 5 days after rainfall (Kiesow 2015), indicating that other season-specific factors also may contribute to the cuing of breeding.

Monsoonal rainfall events in the region are typically highly localized and strongly affected by local meteorological conditions, and their spatial distribution varies both within and between years. Consequently, the magnitude and timing of such events can vary greatly from one locality to the next as well as from one year to the next. The timing and spatial distribution of CRTO breeding therefore vary widely both within and between years. In fact, little or no breeding may occur in

an individual locality in an individual year if the highly variable monsoonal rainfall fails to materialize in that locality that year (Leavitt et al. 2017; Miller and Cotten 2016; O'Donnell and Leavitt 2017a, 2017b; Sullivan and Fernandez 1999), or if suitable conditions of temperature and humidity do not also occur (Kiesow 2015). LCR MSCP (2016) notes, "Sullivan and Fernandez (1999) observed the persistence of CRTO over a 6-year time period in the absence of successful breeding through many seasons."

When they do breed, CRTO females deposit approximately 7,500–8,000 eggs in a single mating event. The eggs mature and hatch within 1 to 2 days, and the resulting larvae also mature very quickly, completing their metamorphosis in a month or less, an unusually rapid maturation for an amphibian (see chapter 2). This rapid maturation reduces the risks of the seasonal pools stagnating or drying completely before the young can complete their metamorphosis and disperse to their adult, terrestrial habitat. This combination of breeding cued by temporally and spatially limited hydrologic conditions, production of large egg masses, and rapid maturation to metamorphosis fits the concept of "explosive breeding" defined by Wells (1977) as an expected characteristic of anurans in desert environments.

CRTO adults live in abandoned rodent burrows and similar shallow underground settings dispersed within a few hundred meters of permanent or seasonal water bodies, including seasonal water bodies that do not receive water every year. From May through August they are active only at night, and they stay in their burrows both day and night from September to April. The literature on CRTO discusses, but does not provide, systematic evidence for the physiological adaptations involved in this period of dormancy. The long duration of CRTO dormancy through the (relatively) cooler months of the year is consistent with their status as one of the few species in their mostly tropical genus of Central America bufonids with ranges that extend northward into the Southwestern United States.

CRTO reproductive ecology thus may be understood as an adaptation to a unique set of environmental constraints of temperature and highly variable precipitation in a desert environment by a member of a tropical genus with a core reproductive strategy of placing eggs in temporary or permanent puddles and ponds during the rainy season (Mendelson, III et al. 2011).

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 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 the hypotheses well tested, but others less so. Scientists and managers can then identify which hypotheses and the assumptions they express most strongly influence management actions. A CEM thus helps inform 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. A 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, a 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. A CEM then identifies the factors that shape the rates of these outcomes in the study area and thereby shape the abundance, distribution, and persistence of the species in that area.

The CRTO 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) (LCR MSCP 2004) and annual work plans (e.g., LCR MSCP 2018a). The process also follows conventions for life history CEMs focused on individual species and their population dynamics in the relevant branch of zoology for the species of interest. Further, the process is guided by an overarching need to ensure that the CEM helps the LCR MSCP identify areas of scientific uncertainty concerning the ecology and specific habitat requirements of the species it has been charged with conserving, the effects of specific stressors on these species, the effects of specific management actions aimed at habitat and species conservation, and the appropriate methods with which to monitor species and habitat conditions. Each CEM is developed in consultation with experts in the LCR MSCP, and submitted in draft form for review by the LCR MSCP, to ensure that the CEM meets management needs. Terminology for life stages, life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors is standardized across CEMs where feasible and appropriate.

The process of identifying the life stages for a CEM recognizes that the life cycle of any species can be divided into multiple life stages. There is no rule for how many life stages a CEM must include, and different scientists may lump together or divide up the life cycle into a different set of life stages. The process of identifying the life stages for the LCR MSCP conceptual ecological models takes into account the following two criteria for lumping versus splitting life stages. First, knowledge of the species in the Lower Colorado River Valley prior to river

regulation and the general ecological literature for similar species indicates that there could be differences in habitat requirements, threats, behaviors, or management requirements for individuals in different portions of the life cycle. Second, a single life stage may encompass several age classes. However, unless there are strong ecological reasons to distinguish individual age classes or groups of age classes as separate life stages, the LCR MSCP conceptual ecological models combine different age classes into the fewest life stages that make good ecological sense.

The process of identifying the life-stage outcomes for a CEM follows the conventions for life history CEMs focused on individual species and their population dynamics in the relevant branch of zoology for the species of interest as noted above. These conventions recognize three possibilities: (1) The outcomes for an individual life stage may consist exclusively of survival. For example, the outcome of a juvenile life stage may consist only of survival to become an adult. (2) The outcomes for an individual life stage may consist of both survival and participation in reproduction, when participation in reproduction constitutes a distinct life stage for the species. (3) Alternatively, the outcomes for an individual life stage may consist of both survival and fertility, the latter of which concerns the production of viable fertilized eggs in the absence of parental 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 focus of this CEM is 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 they 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, CEMs lump together properties of the physical or biological environment that have similar effects or management implications across multiple life stages even if these effects or implications differ in their details between life stages. Lumping together such closely related properties under the heading for a single habitat element across all life stages makes comparison and integration of the CEMs for the individual life stages across the entire life cycle less difficult. On the other hand, a CEM may split properties of the physical or biological environment into separate habitat elements if they do not meet any of these criteria.

Finally, the process of identifying the controlling factors for each life stage in a CEM focuses on environmental conditions and dynamics—including human actions—that (1) determine the quality, abundance, and spatial and temporal distributions of important habitat elements and (2) are within the scope of potential human manipulation, most particularly manipulation by the LCR MSCP and its conservation partners along the Lower Colorado River Valley. The specific or “immediate” controlling factors identified in a CEM necessarily exist and vary in a larger context of human institutions and policies and both short- and long-term dynamics of climate and geology. However, a 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, 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 CEMs across the LCR MSCP less difficult.

Each CEM not only identifies these five components (life stages, life-stage outcomes, critical biological activities and processes, habitat elements, and controlling factors) for each species, it also identifies the causal relationships among them that affect life-stage outcome rates. Further, a 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.

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

Chapter 2 – CRTO 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 CRTO within the greater LCR ecosystem on which to build the CEM. Except where noted, the sources for the following information are AmphibiaWeb (2019), which updates information from Fouquette, Jr. et al. (2005); LCR MSCP (2016); Nafis (2019); NatureServe (2019); Sullivan and Fernandez (1999); and Thomson et al. (2016). Table 1 and figure 1 summarize the proposed CRTO life stage model.

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

Life stage	Life-stage outcomes
1. Eggs	• Egg (embryo) growth • Egg survival
2. Larvae and metamorphs	• Larval-metamorph growth • Larval-metamorph survival
3. Adults	• Adult growth • Adult survival • Adult fertility • Gene flow

INTRODUCTION TO THE COLORADO RIVER TOAD LIFE CYCLE

The CRTO life cycle is typical of many amphibians, with aquatic egg (embryo), hatchling, and larval phases, each with its own distinctive suite of behaviors and developmental transformations, followed by metamorphosis to an adult 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 CRTO conceptual ecological model combines the hatchling, larval, and metamorph developmental stages of Gosner (1960) and McDiarmid and Altig (1999) into a single life stage. The authors of this CEM considered distinguishing these developmental stages as separate life stages; however, they found no separate information on these developmental stages in the

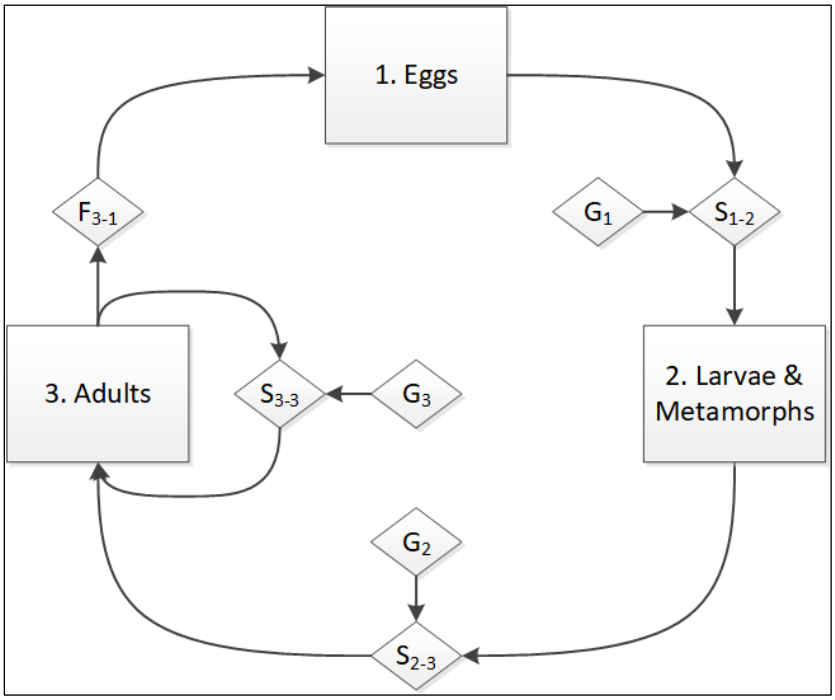

Figure 1.—Proposed CRTO life history model.
Explanation of figure 1: Squares indicate life stages, diamonds indicate life-stage outcomes, and arrows indicate life-stage transitions. In the diamonds, S = survival, G = growth, F = fertility, and subscripts indicate the life stages involved in each transition.

published literature on CRTO and no ecological justifications for making these distinctions in the CEM. Evidence in the future may support such finer distinctions.

The CRTO 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 occur at different rates in females versus males. "Survival" for eggs and larvae-metamorphs in the CRTO 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 CRTO conceptual ecological model refers to the rate at which individuals in a local population survive from year to year. CRTO are estimated to have a maximum life span of 4 to 5 years in the wild (see below).

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

COLORADO RIVER TOAD LIFE STAGE 1 – EGGS

The CRTO eggs life stage begins when adult females deposit their eggs in a shallow, still or very-low-velocity, permanent or seasonal water body. Breeding (including breeding site selection, mate attraction and selection, amplexus, fertilization, and ovipositing) is a critical biological activity or process in the adults life stage, discussed below. The CRTO egg stage ends when the embryos emerge from their natal egg mass as hatchlings, which this CEM addresses as part of the succeeding larvae and metamorphs life stage as noted above. The literature reviewed for this CEM provides only one observation on the duration of the eggs life stage. Cotten and Leavitt (2016) report from monitoring in the Agua Fria River valley in Arizona in 2014 that "…all of the Adobe Dam (lower Skunk Creek) egg masses correlated with a heavy rain and flood on August 19. Egg masses were dissolving, in most cases, and tadpoles free swimming in 24–36 hours." The brevity of the CRTO eggs life stage is consistent with evidence that the entire sequence from oviposition to the completion of metamorphosis in CRTO spans a month or less (see below, this chapter).

CRTO egg masses consist of long jelly-like tubes, with each female depositing approximately 7,500–8,000 eggs in a single mating event. However, such events may not take place every year in every locality (see below, this chapter). As a result, average annual egg deposition per female may be less.

CRTO may leave their egg masses loosely attached to submerged living vegetation or plant litter or simply stretched across the top of the substrate (Cotten and Leavitt 2016; Leavitt et al. 2017). Portions of egg masses may become exposed by a drop in water level, resulting in desiccation and mortality (Cotten and Leavitt 2016). However, CRTO egg masses that are not firmly attached to non-floating materials presumably may remain submerged through at least some changes in water depth. Further, the rapid maturation of CRTO eggs to hatching minimizes the length of time when they are vulnerable to changes in water depth. The literature reviewed for this CEM provides no information on hatch success rates for CRTO egg masses.

Other species presumably consume CRTO 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

and larvae. These findings are consistent with reports worldwide of crayfish as predators of amphibian eggs and larvae. All species that consume CRTO larvae (see below, this chapter) potentially could consume CRTO eggs as well. The discussions of arthropods and vertebrates in chapter 4 further address possible predators of CRTO eggs.

CRTO eggs may be unpalatable or toxic to some predators. As discussed later in this chapter (see "Colorado River Toad Life Stage 3 – Adults"), CRTO adults secrete several chemical compounds (indolealkylamines and polypeptides) that are unpalatable or toxic to vertebrate predators, a common feature of bufonids. Such toxins may be present in bufonid eggs and tadpoles as well (Hayes 1989). However, the literature reviewed for this CEM does not address such potential unpalatability or toxicity specifically in CRTO eggs.

The literature reviewed for this CEM also does not specifically discuss other factors that could affect CRTO egg development. Among anurans in general, embryos are vulnerable to predation, infection and parasites, solar radiation and/or exposure, dehydration, displacement or burial by a flood pulse, elevated water temperatures, or reduced concentrations of dissolved oxygen (Alford 1999; Duellman and Trueb 1986). Effects from these stressors may include delayed development or outright mortality. For example:

- The rate of maturation of eggs in other frog and toad species in the region varies with water temperature (Zweifel 1968), but the literature reviewed for this CEM found no studies that investigate the topic for CRTO.

- The presence of high salinities in the waters of the LCR is an ongoing concern for the LCR MSCP (LCR MSCP 2018a, 2018b). Among anurans in general, including many bufonid species, eggs and larvae exposed to salinities above approximately 2 to 3 parts per thousand experience increasing proportions of developmental abnormalities and fatalities, with exposures above approximately 5 to 10 parts per thousand almost always resulting in death (Albecker and McCoy 2017; Hall et al. 2017; Hopkins and Brodie 2015; Kefford et al. 2016; Stănescu et al. 2017; Woolrich-Piña et al. 2017). Hopkins and Brodie (2015) systematically reviewed the literature on the impacts of salinity on amphibians worldwide across all life stages and found no studies of CRTO and only two focused on other species in the genus *Incilius*. The literature review for this CEM did not identify any subsequent studies of the topic for CRTO.

- The presence of selenium in the waters of the LCR is also an ongoing concern for the LCR MSCP (LCR MSCP 2018a, 2018b). Anurans in general are highly sensitive to exposure to selenium in the water and in the foods they consume, and adults can bioaccumulate the element to concentrations that result in both sublethal and lethal effects

(U.S. Environmental Protection Agency [EPA] 2016). However, neither the literature reviewed by the EPA to develop its aquatic water quality criteria for selenium (EPA 2016) nor the literature reviewed for this CEM contain information on selenium sensitivity in CRTO or any closely related species in any life stage.

The lack of information on such susceptibilities in CRTO in any life stage indicates potentially important gaps in knowledge, given the general susceptibility of anurans to physiological and developmental harm from exposure to unsuitable ranges of water temperatures and chemical composition.

Growth and survival through the eggs life stage, among anurans in general, also can vary with the behavior and condition of the female parent. As discussed below, this chapter, female age and body size affect clutch size in anuran species (Stebbins and Cohen 1995; Wells 2007 and references therein). 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 investigations have looked for these possible interactions specifically for CRTO.

Colorado River Toad Life Stage 2 – Larvae and Metamorphs

The CRTO larvae and metamorphs life stage begins when the eggs hatch and the new larvae (hatchlings) swim away from the remains of their natal egg mass as tadpoles with eyes, a tail, and external gills. CRTO undergo several types of transformations during this life stage, culminating in a final metamorphosis into adults. CRTO larvae can reach lengths (SVL) of 57 mm before beginning their final metamorphosis. The CRTO larvae and metamorphs life stage ends with the completion of metamorphosis, which involves significant hormonal and physical changes. Beginning with the emergence of both hind limbs and forelimbs, the legs continue to develop as the tail disappears; bone replaces cartilage; the shape of the skull, and particularly the jaw, changes to an adult morphology; lungs develop in place of gills; and the digestive system transforms to accommodate a change in diet from herbivory to carnivory (Duellman and Trueb 1986; Gilbert 2000; Wells 2007).

The authors of this CEM considered distinguishing the final phase of metamorphosis as a separate “metamorph” life stage for two reasons. First, anurans undergoing their final metamorphosis do not forage, as do anuran larvae and adults, but rather obtain all their nutrition through resorption of their tails. Second, anuran metamorphs undergoing their final metamorphosis are particularly vulnerable to predation due to their “diminished locomotor capacity”

(Hoff et al. 1999; Wassersug and Sperry 1977). Duellman and Trueb (1986) note that, while larval survivorship in amphibians is low in general, the transformation through metamorphosis is particularly challenging. However, the literature reviewed for this CEM does not provide information on CRTO metamorphs—let alone threats to them—separately from information on CRTO larvae and, in fact provides little information on CRTO larvae or metamorphs at all. Consequently, while evidence in the future may support distinguishing a CRTO metamorph life stage separately from the larval life stage, this CEM addresses them together.

The literature reviewed for this CEM provides no information on survival rates among CRTO larvae and metamorphs. It also provides little information on the duration of the CRTO larvae and metamorphs life stage, except to note that it spans a month or less. The LCR MSCP species account (2016) notes,

> *"Little is known about the length of development of eggs, larvae, or tadpole except that it takes less than 30 days for an egg to metamorphose into a froglet (Musgrave and Cochran 1930; Brennan and Holycross 2006). When compared to other frogs and toads, Colorado River toads develop from zygotes to hatchlings at a remarkably fast rate (Musgrave and Cochran 1930; Brennan and Holycross 2006)."*

CRTO larvae are completely aquatic. As with all anuran 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. The literature reviewed for this CEM provides no information on CRTO larval diet. CRTO larvae are assumed to be algivorous or omnivorous based on larval diets in related species (Fouquette, Jr. et al. 2005). As noted above, anuran metamorphs do not forage at all.

The literature reviewed for this CEM also provides no information on predation on CRTO larvae or metamorphs, but it does provide information pointing in possible directions for investigation. Specifically,

- 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 et al. 2015; Cotten and Grandmaison 2013; 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 several anurans. Cotten et al. (2015) note that the frequency of captures of this gartersnake in funnel traps along the Bill Williams River in 2012 increased during amphibian metamorphosis. However, the literature on the northern Mexican gartersnake in the region does not specifically identify CRTO larvae or metamorphs as prey.

- American bullfrog (*Rana = Lithobates catesbeiana*) larvae and adults and the non-native northern crayfish are widely suspected as predators of anuran larvae in the region (Sredl et al. 1997b). Similarly, as noted earlier in this chapter, the non-native virile or northern crayfish also is known to prey on Arizona native amphibian eggs and larvae (Fernandez and Rosen 1996). Other species known to prey on amphibian larvae in the region include aquatic insects and their larvae, native and non-native fishes, the Rio Grande leopard frog (*Rana = Lithobates berlandieri*), tiger salamanders (*Ambystoma tigrinum*), mud turtles (*Kinosternon sonoriense*), great blue herons (*Ardea herodias*), Yuma clapper rails (*Rallus longirostris yumanensis*), and least bitterns (*Ixobrychus exilis*) (Braun et al. 2020; Sredl et al. 1997a). CRTO larvae in isolated, seasonal pools may face fewer of these kinds of predators than CRTO larvae in permanent water bodies (see chapter 3, "Predation"). However, some aquatic predatory arthropods may colonize or become active and mature rapidly in temporary desert pools (Griffis-Kyle et al. 2019). Chapter 4 (see "Arthropod Community" and "Vertebrate Community") further addresses possible predators of CRTO larvae and metamorphs.

Understanding of predation on CRTO larvae and metamorphs, as with CRTO eggs, again must take into account the possibility that they are unpalatable or toxic to some predators. As noted above, toxins present in bufonid adults may be present in their eggs and tadpoles as well (Hayes 1989). On the other hand, the quantities of toxins present in some toad species and their composition may change as each individual toad matures (Toledo and Jared 1995). The literature reviewed for this CEM does not address such potential toxicity or its maturation in CRTO larvae or metamorphs.

The literature reviewed for this CEM does not discuss other factors that could affect CRTO larval or metamorph development or survival. As noted above, anuran larvae in general are vulnerable to predation, infection and parasites, solar radiation and/or exposure, dehydration, displacement or burial by a flood pulse, elevated water temperatures, or reduced oxygen levels (Alford 1999; Duellman and Trueb 1986). Effects from these stressors may include delayed development or outright mortality. CRTO and other toads hatched into isolated, seasonal pools would be particularly vulnerable to effects associated with water stagnation and evaporation (Griffis-Kyle et al. 2019). As noted above for CRTO eggs, CRTO larvae and metamorphs may be sensitive to exposure to elevated salinity and selenium concentrations as well, and evaporation from seasonal pools would increase salinity and selenium concentrations as the pools dry. Again, however, the literature reviewed for this CEM does not address any of these topics. As also noted above, the lack of information on such sensitivities in CRTO in any life stage indicates potentially important gaps in knowledge, given the general susceptibility of anurans to physiological and developmental harm from exposure to unsuitable ranges of water temperatures and chemical composition.

COLORADO RIVER TOAD LIFE STAGE 3 – ADULTS

The CRTO adults life stage begins with the completion of metamorphosis and lasts through the remainder of the toad's life (see discussion of CRTO longevity, below). CRTO adults initially are sexually immature and reach sexual maturity only after additional growth and hormonal changes. Enderson (2019) notes that sexually immature CRTO "…bear little resemblance to adults and are often confused for red-spotted toads (*Bufo punctatus*)." The literature reviewed for this CEM includes only one study that produced information on how quickly CRTO reach sexual maturity: Sullivan and Fernandez (1999) collected data on age structure and growth as well as information on breeding behaviors in CRTO and three other Arizona toads—the Great Plains toad (*Bufo cognatus*), red-spotted toad, and Couch's spadefoot toad (*Scaphiopus couchii*)—at two breeding sites in north-central Phoenix during the summer monsoon seasons of 1990–95. The authors carried out "…a skeletochronologic analysis of lines of arrested growth in digits and femurs," which found that, among the CRTO gathered for breeding at the two sites in 1994 and 1995, the youngest individuals participating in reproductive activity were 2 years old.

Fouquette, Jr. et al. (2005) give the following SVL size ranges for CRTO adults at sexual maturity: "Males, 80–156 mm; females, 87–178 mm (Wright and Wright 1949 *in* Fouquette, Jr., et al. 2005). Adults may be as large as 190 mm (Degenhardt et al. 1996; Heringhi 1969 *in* Fouquette 1970)." Fouquette, Jr. et al. (2005) also provide estimates of the CRTO maximum lifespan, noting the estimate of 4 years from the study of breeding adults by Sullivan and Fernandez (1999; see above) but also noting,

> *"Conant and Hudson (1949) cited a record of 2 yr (and 0 mo) in captive toads, while Snider and Bowler (1992) reported a wild-caught adult lived 15 yr, 5 mo, 16 d in captivity; however, based on data from other bufonids, longevity in nature is likely to be at least 4–5 yr."*

Sullivan and Fernandez (1999) concluded that the results of their study of CRTO at breeding sites "…indicate rapid growth to maturity but do not support the notion that these anuran amphibians are long-lived organisms that exhibit an extended reproductive lifespan as adults in response to a highly variable, harsh desert environment."

The LCR MSCP (2016) further reports,

> *"Sullivan and Fernandez (1999) found SVL to be positively correlated with body mass for males. SVL and age, estimated by lines of arrested*

> *growth, were not significantly correlated in a population in Maricopa County, Arizona (Sullivan and Fernandez 1999). Growth rates appear to decrease with age (Sullivan and Fernandez 1999).”*

When they are not seasonally dormant (see below, this chapter), CRTO adults are active and hunt only at night. The species is known as “…a voracious predator that may be able to consume anything it can overcome, including other amphibians.” The LCR MSCP species account (2016) summarizes the literature on the CRTO adult diet as follows:

> “[They] *are active foragers and feed on invertebrates, lizards, small mammals, and amphibians (Brennan and Holycross 2006). A stomach content analysis of five specimens and an intestinal analysis of one specimen produced members of the following orders, from most abundant to least abundant: beetles (Coleoptera); wasps, ants, and bees (Hymenoptera); termites (Isoptera); sun spiders (Solifugae); true bugs (Hemiptera); butterflies and moths (Lepidoptera); spiders, mites, and scorpions (Arachnida); grasshoppers, locusts, and crickets (Orthoptera), millipedes (Spirobolida); and centipedes (Scolopendromorpha) (Cole 1962). Colorado River toads are able to eat prey that is protected by sting mechanisms or defensive secretions (Cole 1962).*

AmphibiaWeb (2019) specifically mentions CRTO preying on the Great Plains toad and Couch’s spadefoot toad. Bogan and Eppehimer (2017) describe a CRTO that had captured and unsuccessfully attempted to consume a western desert tarantula (*Aphonopelma chalcodes*). Nafis (2019) reports that “Sometimes this toad can be seen sitting at night under a street light, eating passing flying insects.” However, few studies have systematically investigated dietary or foraging behaviors among CRTO adults in general, let alone specifically in the western portions of its historic range.

CRTO breeding involves multiple steps, including breeding site selection, mate attraction and selection, amplexus, fertilization, and ovipositing. Chapter 3 provides a detailed summary of this critical biological activity and process.

CRTO may not reproduce every year. As noted earlier in this chapter, CRTO males and/or females may not aggregate at breeding sites, or may aggregate but not mate, in years with dry monsoon seasons. Such an annual failure occurred in the Bill Williams River valley in 2015 (Leavitt et al. 2017; Miller and Cotten 2016; O’Donnell and Leavitt 2017a, 2017b). The study of two breeding sites near Phoenix in 1990–95 by Sullivan and Fernandez (1999) recorded substantial CRTO breeding activity only in 1990 and 1992, following a series of significant rainfall events in which more than 25 mm of rainfall fell within 24 hours, and a single night of CRTO mating in 1995.

CRTO breeding activity may be highly competitive. Nafis (2019) states that "…the males call to advertise their fitness to competing males and to females." However, Kiesow (2015) reports recording only single CRTO males calling at any single location in Goldwater Range-East in 2012. The literature reviewed for this CEM provides no information on sex ratios in CRTO either in general or at breeding sites in particular.

Growth in anuran adults can affect reproductive output. Wells (2007) reports that the size and age specifically of adult females of many amphibian species affect clutch size. Stebbins and Cohen (1995) report that amphibian clutch size depends in part on genetics, nutritional condition of the female, the number of repetitive breeding events, and the temperature and length of 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, the literature reviewed for this CEM provides no information on such potential biological interactions specifically for CRTO. Similarly, the literature reviewed provides no information on possible effects of adult age or body size on CRTO survival or mating success.

CRTO are not known to migrate, in the sense that they do not abandon entire localities and move systematically to other localities in large numbers either seasonally or over longer periods. However, some works in the literature reviewed for this CEM use the term "migration" to describe more localized movements of CRTO between breeding and non-breeding habitat. This CEM alternatively uses the term, "aggregation/dispersion," to label this type of localized movement: CRTO disperse from their natal sites to non-breeding habitat after completing metamorphosis and remain dispersed and solitary for most of every year for the remainder of their lives. However, once they reach sexual maturity, they also may aggregate briefly and apparently only once per year at suitable water bodies to attempt to mate.

CRTO non-breeding habitat consists of dryland areas close to permanent or predictable water, including ephemeral pools and intermittent water courses (Fouquette, Jr. 1970; Fouquette, Jr. et al. 2005; Griffis-Kyle et al. 2019; Kiesow 2015; Levick et al. 2008). In uplands near seasonal or permanent water courses (e.g., desert washes, arroyos, canyons), such habitat may include areas of rocky, sloping ground (e.g., Griffis-Kyle et al. 2019; Kiesow 2015; Kiesow and Griffis-Kyle 2017). Near lowland water courses, such habitat may include larger areas of floodplain or similar lowland soils (Cotten and Leavitt 2016; Leavitt et al. 2017; Levick et al. 2008). In the Bill Williams River valley, such lowland habitat "…consists of low elevation, flat, dry, and sandy features dominated by creosote bush (*Larrea tridentata*), white bursage (*Ambrosia dumosa – aka* burrobush), and desert salt bush (*Atriplex polycarpa*)" (O'Donnell and Leavitt 2017b). Elsewhere, CRTO non-breeding habitat may include "rocky riparian zones with sycamore

and cottonwoods, and oak-walnut woodlands in mountain canyons" (Fouquette, Jr. et al. 2005). Chapter 4 (see "Vegetation Assemblage:) further discusses the vegetation in CRTO breeding and non-breeding habitat.

LCR MSCP (2016), discussing CRTO movement distances between breeding and non-breeding habitat, notes that,

> *"…no studies have been conducted on the length of these migrations (NatureServe 2006; Fouquette, Jr. et al. 2005). Individuals may migrate several hundred meters from permanent to seasonal pools following heavy rains (Wright and Wright 1949* in *Fouquette, Jr. et al. 2005). Little research has been conducted on the home range of this species (Fouquette, Jr. et al. 2005)."*

Fouquette, Jr. et al. (2005) also report,

> *"Dan Beck (unpublished data) radio-tracked an adult Colorado River toad for a period of 390 d[ays][5] in the Tucson Mountains, Pima County, Arizona. During that time activity centered around the release site, although movements of > 400 m were noted in a single day."*

The literature reviewed for this CEM provides no information on possible breeding site fidelity among CRTO and no information on possible genetic homogeneity or fragmentation across their geographic range. Consequently, the literature provides no information on the extent to which their routine aggregation at breeding sites and dispersion to non-breeding habitat together maintain gene flow across this range. The literature also provides no information on the extent to which topography and drainage patterns may affect patterns of aggregation and dispersion.

CRTO may occasionally hybridize with other toads. Fouquette, Jr. (1970) states,

> *Blair (1959) experimentally crossed male* alvarius *with females of three other* Bufo *species. Hybrid larvae from female* B. woodhousii *proceeded to metamorphosis; those from female* B. valliceps *and* B. debilis *stopped at gastrula…Blair (1956) suggested size difference is probably the primary mechanism inhibiting breeding between* alvarius *and other desert toads. A natural hybrid of* alvarius X cognatus *(Ariz. State Univ. No. 2601) indicates that size is not a completely effective barrier to interbreeding."*

[5] "390" may not be the correct number. Fouquette, Jr. et al. (2005) elsewhere state that the tracking took place between September 26, 1988, and June 17, 1989, a span of 264 days.

Similarly, Gergus et al. (1999) report observations of three hybrids between CRTO and a Woodhouse's toad (*Anaxyrus woodhousii*) in central Arizona in in 1959, 1995, and 1997. Gergus et al. (1999) also found that,

> *"Fossil evidence suggests some genomic compatibility has been retained between* B. alvarius *and* B. woodhousii *despite at least 6 million years of independent evolution. Hybridization among members of Bufo may be due to alternative mating tactics of males, such as active searching, and by alteration of historical habitats in central Arizona."*

However, Gergus et al. (1999) did not note whether any of the three hybrids they examined were potentially fertile, and no subsequent studies have reported other such hybrids. Mendelson, III et al. (2011) note that bufonids other than those in the genus *Atelopus* are widely viewed as "…rampant hybridizers both in the lab and in the wild," but that genetic and morphological studies find little evidence of persistence in any resulting crosses. They conclude, "These lines of evidence, of course, do not indicate that such hybridization does not occur, but are suggestive that it may be rare and/or that these species may be subject to strong negative pre- or post-zygotic selection."

CRTO adults must cope with seasonally high and low temperatures and episodes of extreme hot and cold weather as well as periods of drought. CRTO cope with these environmental conditions in part by staying dormant in their burrows from September to April. Further, Fouquette, Jr. et al. (2005) state,

> *"Degenhardt et al. (1996) suggest that large size and smooth skin may predispose Colorado River toads to desiccation, but there is no experimental evidence for this. Indeed, larger size also means lower surface to volume ratio, thus relatively lower expectation of evaporation. There is no direct evidence for aestivation by the species, and it is not likely that they utilize any form of torpor to any greater extent than other species of Bufo. Dan Beck (unpublished data) radio-tracked an adult Colorado River toad that remained in the same burrow under a railroad tie from 26 September 1988–17 June 1989. Body temperature during that time ranged from 11.7 ˚C–29.7 ˚C. It is possible that during part of that period below the surface the toad may have been in a state of torpor or aestivation."*

However, the literature reviewed for this CEM does include any investigations of the topics of CRTO dormancy, aestivation, torpor, or other adaptations to risks of thermal stress or desiccation. As noted above, CRTO also may fail to reproduce in a given locality in years when suitable weather conditions do not occur during the normal breeding season.

CRTO have evolved a range of anti-predator defenses. The large size of CRTO adults may protect them from the attentions of some predators. CRTO adults are well known for the neurotoxins they secrete from prominent parotoid glands on both sides of the back of the head and from other functionally similar glands, including on the dorsal surfaces of all four limbs. CRTO may flee when disturbed, but if confronted, "… individuals are known to inflate their bodies and orient the parotoid glands toward the threat while making a hissing sound" (Gutiérrez-González et al. 2016). Some authors refer to this defensive orientation as a head butting pose. CRTO secrete their toxins when grasped in the mouths of would-be predators, resulting in possible effects to the attacker ranging from discomfort and disorientation to death (see also Gutiérrez-González et al. 2016; Hayes 1989; Toledo and Jared 1995). As noted above (see earlier life stages), the quantities of toxins present and their composition in at least in some toad species can change as the individual matures (Toledo and Jared 1995). However, the literature reviewed for this CEM does not address whether the quantities or potency of toxic secretions change as CRTO adults mature. The CRTO toxic secretions include hallucinogenic compounds, resulting in attention from recreational drug users and, according to Gutiérrez-González et al. (2016), also from practitioners of alternative medicine (e.g., for treating addictions).

Experiences with CRTO toxic secretions presumably discourage would-be predators. Gutiérrez-González et al. (2016) report several instances in which potential predators approached and then moved away from CRTO adults. However, at least a few vertebrates have found ways to prey on CRTO adults either by avoiding or tolerating their secretions (Gutiérrez-González et al. 2016). Chapter 4 (see "Vertebrate Community") discusses the ways in which these vertebrates may do so and identifies other vertebrates that potentially also could prey on CRTO adults. Chapter 3 (see "Predation") discusses other aspects of CRTO biology and behavior that may help it avoid, escape, defend against, or counterbalance losses from predation.

The literature reviewed for this CEM does not indicate whether adult CRTO are sensitive to salinity in their environment. They spend little time in water other than during their brief breeding episodes. It is also possible that, if they are sufficiently sensitive to water salinity, they may avoid breeding in water bodies that they found unsuitably saline. Salt-crusted soils surrounding a water body might also be irritants underfoot. On the other hand, Kiesow and Griffis-Kyle (2017) and Griffis-Kyle et al. (2019) report that, when selecting breeding sites, red-spotted toads and apparently also CRTO and Couch's spadefoot toads simply select the closest available water even if that water has harmful chemical constituents (e.g., a high concentration of ammonia). The drive to breed and the scarcity of water may result in the use of water bodies with poorer habitat quality. However, again, there is no documentation of the topic for CRTO.

As noted earlier in this chapter, anurans in general are highly sensitive to exposure to selenium in the water and in the foods they consume, and adults can bioaccumulate the element from their foods to concentrations that result in both sublethal and lethal effects (EPA 2016). CRTO spend little time in water other than during their brief breeding episodes but may consume arthropods that have aquatic life stages. However, neither the literature reviewed by the EPA to develop its aquatic water quality criteria for selenium (EPA 2016) nor the literature reviewed for this CEM contains information on selenium sensitivity in CRTO or any closely related species in any life stage.

The literature reviewed for this CEM contains little information on diseases among CRTO. The LCR MSCP (2016) notes,

> "*Parasites known to affect Colorado River toads include* Aplectana itzocanensis, Oswaldocruzia pipiens, Physaloptera spp., Physocephalus spp., *and* Rhabdias americanus *of the phyla Nemotoda and* Nematotaenia dispar *of the family* Cestoidea *(Goldberg and Bursey 1991)."*

Helmick et al. (2018) report on investigations of disease in five captive CRTO, in which they found no evidence of exposure to chytrid fungus but did find evidence of novel *Brucella* bacterial infections. The relevance of these findings for CRTO in the wild is unknown. The literature reviewed for this CEM otherwise does not report identifications or outbreaks of chytrid fungus among CRTO anywhere, even in localities where it affects other anurans (Rosen and Caldwell 2004).

The published literature thus provides many suggestions and anecdotes concerning factors that may affect CRTO adult growth, survival, aggregation and dispersion, breeding, or fertility. However, the literature documents few concerted studies of these topics, leaving significant gaps in knowledge to inform resource managers.

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. That is, the rates or intensities of these activities and processes together determine the rates of growth and survival in every life stage and the rate of fertility in the adults life stage.

The descriptions of the three CRTO life stages in chapter 2 identify 10 types of critical biological activities and processes affecting 1 or more CRTO life stages. Some of these types of 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 10 critical biological activities and processes identified in this CEM and their distribution across life stages. The authors considered including an additional critical biological process, hybridization, but determined that there was no need to include this process for the reasons noted in chapter 2 (see discussion of the CRTO adults life stage).

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

Life stage ➔ Critical biological activity or process ⬇	Eggs	Larvae and metamorphs	Adults
Aggregation/dispersion			X
Breeding			X
Chemical stress	X	X	X
Competition		X	X
Disease	X	X	X
Foraging		X	X
Mechanical stress	X	X	X
Predation	X	X	X
Resting/hiding		X	X
Thermal stress	X	X	X

Except where noted, the sources for the following information are AmphibiaWeb (2019), which updates information from Fouquette, Jr. et al. (2005); LCR MSCP (2016); Nafis (2019); NatureServe (2019); Sullivan and Fernandez (1999); and , Thomson et al. (2016). These publications summarize all earlier studies. Where appropriate and accessible, those earlier studies are directly cited, as are several more recent publications on specific investigations. The following paragraphs discuss the 10 critical biological activities and processes in alphabetical order.

AGGREGATION/DISPERSION

As noted in chapter 2, CRTO are not known to migrate; however, adult CRTO exhibit a regular pattern of aggregation and dispersion. They disperse from their natal sites to non-breeding habitat after completing metamorphosis and remain dispersed and solitary for most of every year for the remainder or their lives. The literature reviewed for this CEM does not address the extent to which CRTO disperse across non-breeding habitat or the factors that may shape this extent. As with other amphibians (Duellman and Trueb 1986), these factors may include the availability of food and resting/hiding habitat (see below, this chapter, “Foraging” and “Resting/Hiding”).

Once CRTO adults reach sexual maturity, they episodically interrupt their dispersed occupancy to aggregate briefly at suitable water bodies to attempt to mate. Such aggregation may occur only once per year, and CRTO are known to forego such activity entirely in the absence of suitable environmental cues. The literature reviewed for this CEM identifies the most important such cue as the occurrence of rainfall greater than 25 mm within a 24-hour period (Sullivan and Fernandez 1999; Sullivan and Malmos 1994). However, CRTO also sometimes may gather at potential breeding sites before the onset of rainfall (Fouquette, Jr. 1970), indicating that other season-specific factors may also contribute to the cuing of breeding. Kiesow (2015) found that CRTO breeding activity is also cued secondarily by the occurrence of suitable air temperatures accompanied by elevated humidity (see this chapter, “Breeding,” and chapter 4, “Temperature” and “Water Availability”). The literature reviewed for this CEM does not evaluate whether CRTO adults may attempt to breed more than once per year.

CRTO adults may travel “several hundred meters” (Fouquette, Jr. et al. 2005) between their dispersed residences (e.g., burrows) and their breeding sites. However, the literature reviewed for this CEM does not include any studies that systematically tracked multiple adult CRTO to quantify the scale of such movement or that evaluated the density of CRTO adults across non-breeding habitat. The literature reviewed for this CEM also provides no information on possible breeding site fidelity among CRTO nor information on the extent to which their routine aggregation at breeding sites and dispersion to non-breeding

habitat together maintain gene flow across this range. However, as noted above (see discussion of adults, chapter 2), red-spotted toads and apparently also CRTO and Couch's spadefoot toads seeking breeding sites may simply select the closest available water even if that water has harmful chemical constituents (e.g., a high concentration of ammonia) (Griffis-Kyle et al. 2019; Kiesow and Griffis-Kyle 2017). Such behavior would limit the distances over which individual toads move to mingle at breeding sites.

It is also possible that CRTO select breeding sites not only based on proximity but on cues to the likelihood that the water at a site will persist long enough for eggs to hatch and larvae to metamorphose. Hints of this possibility are found in statements by O'Donnell and Leavitt (2017a, 2017b; see also Miller and Cotten 2016) concerning the feasibility of using funnel traps to capture CRTO in the Bill Williams River valley:

> *"Water evaporating or percolating in 1 or 2 nights prevented [funnel] trapping in potential breeding pools on additional plots other than the two main pools found on Plots 5 and 6. Water was likely available temporarily within the study area other than on Plots 5 and 6, corresponding with rain events, but the inability to get to the study site, coupled with percolation and evaporation, prevented confirmation of this. Successful breeding could not have occurred in these areas because the water did not persist for more than 1 day, and larvae can take up to 1 month to metamorphose (Fouquette et al. 2005). During the 2015 season, there were no monsoon events large enough to create surface water or to encourage a breeding event, so [funnel] traps were never set."*

BREEDING

CRTO breed at night in a process involving multiple steps, including breeding site selection, mate attraction and selection, amplexus, fertilization, and ovipositing. The LCR MSCP (2016) summarizes the literature on this suite of behaviors and its possible environmental cues as follows:

> *"Colorado River toads breed from May through August in ponds, slow-moving streams, temporary pools, or manmade structures that hold water (Stebbins 1985; NatureServe 2006). In Arizona, they usually breed in temporary pools formed by monsoon rains (Brennan and Holycross 2006). In a study conducted at flood control sites in north central Maricopa County, Arizona, rainfall greater than 25 mm within a 24-hour period was necessary for populations of this species to initiate breeding and chorusing activity (Sullivan and Fernandez 1999; Sullivan and Malmos 1994). Breeding and chorusing activity usually occurs one to three nights*

following rainfall events (Sullivan and Fernandez 1999; Sullivan and Malmos 1994). However, Fouquette (1970) and Arnold (1943) observed that while breeding activity is stimulated by rainfall, it is not necessary for reproductive activity. Sullivan and Fernandez (1999) observed the persistence of Colorado River toads over a 6-year time period in the absence of successful breeding through many seasons.

Males use two strategies for pairing with females, including active searching and stationary calling from shallow water. The strategy chosen appears to be influenced by the size of the individual (Sullivan and Malmos 1994). Sullivan and Malmos (1994) noticed that males observed calling were significantly larger than those observed actively searching. When there are fewer males in a breeding aggregation, individuals call more frequently (Sullivan and Malmos 1994). Blair and Pettus (1954) observed that the call of Colorado River toads does not play a role in breeding behavior; however, Sullivan and Malmos (1994) demonstrate in preliminary trials that females were attracted to the call of males. Further research on mate selection techniques needs to be conducted.

The Colorado River toad advertisement call consists of an emphasized note followed by three progressively weaker notes. The fundamental frequency of the advertisement call is 1,096 cycles per second, and the duration is approximately 0.7 second in length (Blair and Pettus 1954). Sound pressure levels of advertisement calls are approximately 88 decibels at about 0.5 meter, similar to other bufonids (Sullivan and Malmos 1994). Release calls consist of a series of pulse groups lasting about 1 second. Advertisement and release calls differ in temporal structure (Sullivan and Malmos 1994). Release calls have a faster pulsation rate and a lower frequency than advertisement calls (Sullivan and Malmos 1994). The frequency or duration of advertisement or release calls is not related to body size or body temperature of individuals (Sullivan and Malmos 1994). The pulse rate of advertisement calls increases as the body temperatures of individuals increase (Sullivan and Malmos 1994). The pulse rate of release calls decreases as the body temperatures of individuals increase (Sullivan and Malmos 1994). The Colorado River toad arytenoid cartilages are believed to be activated only during production of release calls (Sullivan and Malmos 1994).”

As indicated in these quoted passages, there is some uncertainty concerning the factors that may cue CRTO breeding or the ways in which CRTO may respond to these cues in different circumstances. As noted in chapters 1 and 2, and above, this chapter, CRTO sometimes may gather at potential breeding sites before the

onset of rainfall (Fouquette, Jr. 1970). Taubert (2006) reports observing CRTO in Arizona breeding "…in permanent ponds before the monsoon rains start" but that breeding is more common "…after the first rains in July." Based on records of breeding call activity, Kiesow (2015) determined that CRTO attempted to breed in Goldwater Range-East in 2012 within 5 nights following a rainfall event in the vicinity of an individual pool only when two other conditions also occurred: (1) the nighttime air temperature stood between 23 and 27 °C and (2) the concurrent relative humidity stood between 65 and 100% (see chapter 4, "Temperature" and "Water Availability"). No calling activity occurred at a site if even one of these three conditions did not coincide, even at sites with permanent water.

O'Donnell and Leavitt (2017a, 2017b) observed that CRTO calling and breeding in the Bill Williams River valley in 2014 and 2015 occurred later than during the more typical period of May through August (August 3 to September 17, 2014; September 21–23, 2015). They note that, "On September 21, 2015, a dampening rain hit the study site, and CRTO were found the following 2 nights in an ephemeral pool on Plot 6, the same pool in which toads were observed calling the previous year."

Investigators from the AZGFD (Cotten and Leavitt 2016; Leavitt et al. 2017) attempted to collect data on CRTO oviposition sites in the Agua Fria, Bill Williams, and Verde River valleys in Arizona in 2014 and 2015 to identify consistent properties of these water bodies. The study did not include sites in the main stem Lower Colorado River Valley because previous surveys had found no evidence of CRTO breeding activity there. Cotten and Leavitt (2016) summarize the study methods as follows:

> *"Study areas were initially surveyed prior to the monsoon season to narrow the study area to locations where toad activity was most likely to occur following heavy rainfall. These areas included shallow basins, washes, or impoundments where heavy monsoon rainwater could collect to create an ephemeral pool. These activity areas were then revisited occasionally throughout the field season to attempt to detect breeding behavior… When an oviposition site was located, a series of environmental variables at the site location and at a randomly selected 'non-site' were recorded. Non-sites were selected at random within the habitat based on a random number generator for direction (angle) and distance with a minimum of 1 meter (m) and a maximum of 100 m. Data on clusters of egg masses (multiple egg masses within a 0.01-hectare [ha] radius) and randomly selected 'non-clusters were also recorded.' Environmental variables were collected that may contribute to breeding success at each of these locations."*

Leavitt et al. (2017) describe the results as follows:

> *"While much of the Agua Fria and Verde River sites were saturated and adequately inundated following a single week of rain during the 2014 field season, the 2015 field season was exceptionally dry in these drainages. As a result, the only data that exist on egg mass oviposition site selection for Colorado River toads come from the 2014 field effort. Colorado River toads lay long strings of eggs that can cover a very large area (see figure 3). The data analysis suggests that Colorado River toads select shallow water with no canopy cover for oviposition …Average egg mass oviposition sites were 711.3 cm wide (95% CI 269 cm, 1,382 cm) and 571 cm long (95% CI 58 cm, 1,000 cm). Site descriptions from 2014 suggest that very little selection occurs at the site level; rather, it is at a much larger scale that Colorado River toads are selecting breeding habitat (Cotten and Leavitt 2016). They breed in open canopy water sources that are ephemeral in nature; therefore, any data related to water column depth or pH should be considered as transient variables that do not represent the moment of oviposition."*

At the larger scale of approximately 0.01 to 1.00 hectare (ha), Cotten and Leavitt (2016) found simply that CRTO bred in ephemeral pools and oxbows that were filled by flood pulses following large rainfall events and then remained inundated after the flood waters receded. They also report that,

> *"…The water at each breeding site was extremely turbid. In order to minimize the risk of overlooking egg masses in the murky waters after oviposition, amplectic pairs of toads were monitored closely in the anticipation of reproduction."*

Kiesow (2015) and Kiesow and Griffis-Kyle (2017) measured a slightly different list of characteristics of CRTO breeding sites in Goldwater Range-East in 2012—aspect, shading, surface size, elevation, whether the site was a tinaja or an artificial catchment, and ammonia concentration. Statistical analyses indicated that CRTO presence/absence (as indicated by breeding call activity) did not vary consistently with any of these characteristics. In fact, as noted above (see above, this chapter, "Aggregation/ Dispersion"), CRTO in the study area appeared to select the closest available water for breeding, even if that water had harmful chemical constituents (e.g., a high concentration of ammonia), although the statistical sample size was too small to support a more definitive analysis (Griffis-Kyle et al. 2019; Kiesow and Griffis-Kyle 2017).

Adult amphibians typically 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). Goldberg (2018) used histological methods to examine

reproductive readiness in a sample of 17 adult male, 25 adult female, and 1 juvenile female CRTO collected between 1958 and 1999 from Pima County, Arizona, from the herpetology collection of the Natural History Museum of Los Angeles County. All of the males were undergoing spermiogenesis at the time of their capture: "…June (n = 1), July (n = 11), August (n = 3), September (n = 2)." The females showed greater variation in reproductive readiness: Of 16 adult females collected in July, 15 were "…in 'Ready to Spawn' condition in which mature oocytes predominated;" of 6 collected in August only 3 were ready to spawn; and of 3 collected in September only 1 was ready to spawn.

Among anurans in general, as noted above (see chapter 2 and below, this chapter, "Foraging"), 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, the nutritional condition of the female, the number of repetitive breeding events, and the temperature and length of the growing season, among other factors. However, the literature reviewed for this CEM does not report any studies of these possible interactions in CRTO breeding.

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 anurans, CRTO in one or more life stages likely are vulnerable to chemical stress from several potential sources.

This CEM includes hydration stress as a type of chemical stress. Dehydration causes physiological stress and mortality among anuran species in general. Anuran eggs and larvae must remain immersed to survive and have no means for relocating themselves when their habitat dries out. Anuran metamorphs have only limited capabilities for relocating themselves when their habitat dries. Further, anuran metamorphs may successfully relocate themselves to another body of water only if there is water nearby; however, no other bodies of water may be nearby. As noted in chapter 2, CRTO may breed in seasonal ephemeral pools that are not located near any permanent water; their successful reproduction requires only the persistence of water in a breeding pool long enough for metamorphosis to occur.

CRTO adults live most of their lives dispersed across the landscapes around their natal sites. While they do not live in the water, they do appear to live close to locations of at least seasonal water bodies. As noted in chapter 2, CRTO, when not engaged in breeding activity, typically live within close proximity to permanent or predictable water, including ephemeral and intermittent water

courses (Cotten and Leavitt 2016; Leavitt et al. 2017; Levick et al. 2008). Non-breeding habitat in the Bill Williams River valley in 2014–15 consisted of low elevation, flat, dry, sandy areas dominated by creosote bush, white bursage (*aka* burrobush), and desert salt bush (O'Donnell and Leavitt 2017a, 2017b). The soils in such settings presumably have higher moisture levels than soils further from permanent or seasonal surface water. However, the literature reviewed for this CEM provides no information on soil moisture levels in CRTO non-breeding habitat in general or within CRTO burrows in particular.

CRTO adults also reduce water loss by foraging and breeding only at night. As noted also in chapter 2, CRTO may become dormant, aestivate, or become torpid to reduce their risks of desiccation (and risks of thermal stress; see below, this chapter). However, the literature reviewed for this CEM does not systematically address CRTO adaptations to the risks of hydration stress.

Warming and/or stagnation of water during hot and/or dry weather depress the concentration of DO, potentially stressing toad eggs or larvae (Pinder and Friet 1994). Anuran 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, although the CRTO eggs life stage may be too brief for this factor to affect survival. Warming and/or stagnation also can promote the production of ammonia, particularly in permanent water catchments that accumulate organic matter (Griffis-Kyle et al. 2019). Ammonia is potentially harmful to amphibian larval development, too, but CRTO do not appear to avoid pools with elevated ammonia concentrations (Kiesow 2015; Kiesow and Griffis-Kyle 2017). Drying of small isolated water bodies also can raise salinity. As noted in chapter 2, CRTO eggs and larvae could be sensitive to elevated salinity; however, investigators have not looked into the effects of any of these possible aquatic chemical factors in CRTO egg or larval development or survival.

Amphibians worldwide 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 in amphibian tissue (Bank et al. 2007; Blaustein et al. 2003; Brühl et al. 2013; Davidson et al. 2002; Mann et al. 2009; Smalling et al. 2015; Unrine et al. 2004; EPA 2016). However, the literature reviewed for this CEM does not include any studies of the effects of such pollutants specifically on CRTO or related species in the Southwestern United States. It should also be noted that most observations of CRTO have focused on sites outside areas of significant agricultural, industrial, or urban land use—i.e., on sites where pollutant levels are more likely to be low. However, CRTO have been observed in irrigation ditches in agricultural areas. Agricultural activities are widespread in the LCR valley, particularly along Reaches 4–7, and the LCR itself has elevated salinity and carries a diversity of pollutants (see chapters 4 and 5), including

dissolved selenium, a known threat to anuran reproduction (EPA 2016). As discussed in chapter 2, elevated salinity and selenium concentrations could be harmful to CRTO eggs and larvae, although no studies have been conducted to look into this possibility.

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; levels of UV-B radiation have been rising worldwide (Blaustein et al. 2003). However, investigators have not studied this phenomenon among CRTO.

Chemical stress may be acute or chronic, may directly result in mortality, may impair a range of bodily functions or interfere with embryo or larval development, or may impair reproduction. Once CRTO metamorphose, they presumably become 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 between them and other taxa is common in aquatic systems (Morin 1986; Wells 2007). For example, anuran larvae may compete for food with mosquitoes and with other grazing aquatic invertebrates (Mokany and Shine 2003; Morin et al. 1988).

The intensity of competition for food among anuran larvae in an individual water body presumably depends on both the abundance of potential food items and the density of potential competitors. Resulting constraints on foraging success in anuran larvae potentially can affect their rates of growth and maturation and their sizes as adults (Berven 1990), which in turn potentially affect their fertility and breeding success as adults (Berven 1982; Howard and Kluge 1985). However, the literature reviewed for this CEM does not address these possible competitive interactions or effects in the CRTO larvae and metamorphs life stage.

As discussed above, CRTO breeding activities, including calling and active searching behaviors, appear to be highly competitive and vary with at least male body size; however, the literature reviewed for this CEM provides no information on what factors (e.g., body size, call characteristics, etc.) may affect the ultimate mating success of individual males or females or clutch size and viability.

The literature reviewed for this CEM provides no evidence of competitive exclusion of CRTO from habitat by other species. CRTO have been observed breeding in the same water bodies as other anurans, including Couch's spadefoot, Great Plains, red-spotted, and Woodhouse's toads (Fouquette, Jr. et al. 2005; Kiesow 2015; Kiesow and Griffis-Kyle 2017; LCR MSCP 2016; Sullivan and Fernandez 1999). If anything, CRTO may exclude some of these other toad species from some habitat: As noted in chapter 2, CRTO adults have been reported to feed occasionally on spadefoot and red-spotted toads.

The non-native northern crayfish can reduce aquatic vegetation and increase turbidity (Fernandez and Rosen 1996). These effects can be detrimental to native leopard frogs in the Southwestern United States (Fernandez and Rosen 1996), but the reduction in aquatic vegetation could benefit CRTO, which breed preferentially in water bodies with less aquatic vegetation (see chapter 4, "Vegetation Assemblage"). The literature does not provide information on how CRTO respond to elevated turbidity in breeding waters.

It is also theoretically possible that CRTO adults could face competition for non-breeding, resting/hiding habitat (see chapter 4). As summarized by LCR MSCP (2016),

> *"The habitat for Colorado River toads when dormant, or their refugium during active periods, includes subterranean shelters such as rodent burrows, rock outcrops, or hollows under watering troughs (Wright and Wright 1949* in *Fouquette, Jr., et al. 2005; Lowe 1964* in *Fouquette, Jr., et al. 2005; D. Beck, unpublished data* in *Fouquette, Jr. et al. 2005)."*

Conspecifics and other species may compete for such crucial desert refugia. However, the literature reviewed for this CEM provides no information on this possibility for CRTO.

Every animal species evolves capabilities that permit its persistence despite competition from conspecifics and other species, including behaviors that allow it to avoid, defend against, or compensate for such competition. 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, the literature reviewed for this CEM does not mention any evidence of resource partitioning by CRTO. As noted above, for example, several sympatric toad species may share the use of individual seasonal pools with CRTO for breeding.

DISEASE

All anurans are subject to 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). However, the literature reviewed for this CEM provides no information on disease among CRTO in the wild.

FORAGING

All animal species must acquire nourishment for survival, growth, and reproduction. In CRTO, both larvae and adults obtain their nourishment by foraging for other organisms to consume. Foraging success in CRTO also may affect reproductive output (fecundity): Among anurans in general, larger females typically produce larger clutches (Duellman and Trueb 1986). However, as noted in chapter 2, the available literature provides little information on foraging behaviors, preferences, success rates, or consequences in CRTO larvae or adults.

CRTO presumably begin foraging immediately after they emerge from their eggs and their mouth parts differentiate, stop during their final metamorphosis, and then resume as adults. As noted in chapter 2, CRTO larvae are assumed to be algivorous or omnivorous, based on larval diets in related species (Fouquette, Jr. et al. (2005). No studies in the literature reviewed for this CEM specifically examine CRTO larval foraging behaviors, dietary preferences, or success rates.

Chapter 2 summarizes the little information available on foraging in CRTO adults. Fouquette, Jr. et al. (2005) state,

> *"Colorado River toads are active foragers. Prey includes beetles, grasshoppers, wasps, centipedes, millipedes, ants, termites, solpugids, spiders, snails, scorpions, Great Plains toads, Couch's spadefoot toads, small lizards, and mice (King, 1932; Arnold, 1943; Gates, 1957; Cole, 1962; Degenhardt et al., 1996). Colorado River toads will eat almost any prey they can subdue and ingest, including those with defensive stinging capabilities (Cole, 1962; Degenhardt et al., 1996)."*

CRTO adults forage at night and have been observed "…sitting at night under a street light, eating passing flying insects" Nafis (2019). Since CRTO adults can become quite large—they are the largest toad in the United States, and adults can reach as much as 190 mm SVL and weigh as much as 900 grams (Enderson 2019)—they are able to subdue a wide variety of prey. However, other than the

report of their sitting beneath a street light to capture passing insects, none of the literature reviewed for this CEM documents any specific CRTO foraging behaviors. In fact, as noted in chapter 2, no studies have been conducted to systematically investigate diet or foraging behaviors among adult CRTO adults anywhere, let alone specifically in the western portions of its historic range.

MECHANICAL STRESS

CRTO in every life stage may suffer stress and outright physical destruction due to mechanical impacts, abrasions, and burial. However, the subject apparently has not been studied for CRTO in any life stage.

Situations that could result in mechanical stress to CRTO in their breeding and non-breeding habitats conceivably could include encounters with human foot traffic and vehicles, including agricultural, construction, military, monitoring, and recreational vehicles; entrainment by inescapable flow velocities and turbulence, including from artificial release of water from dams and diversion structures; burial by a rapid influx of sediment in these same high-flow circumstances; unsuccessful predator attacks; or capture during monitoring or private collecting. However, CRTO are likely well adapted to the highly variable hydrology of their native range, including the likelihood of habitat-altering flood pulses (see chapter 1).

Mechanical stress that does not result in mortality nevertheless may leave the affected individuals more vulnerable to infections and mortality from other causes. As with all animals, CRTO larvae, metamorphs, and 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, CRTO adults may seek refuge habitat in such settings (see below, this chapter, and chapter 2). The literature reviewed for this CEM does not document how quickly CRTO adults may be able to move to avoid mechanical hazards. However, Nafis (2019) notes that CRTO adults are “Capable of moving very quickly with huge leaps, and by running across the ground on all four legs.” Compared to adults, CRTO larvae and metamorphs can avoid disturbances only on a limited spatial scale.

PREDATION

CRTO presumably are vulnerable to injury and mortality due to predation during every life stage, as are 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 compensate demographically for losses from predation.

Among anurans in general, predation is greatest on their eggs and larvae (Duellman and Trueb 1986). Potential predators of anuran eggs and larvae 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 similarly wide array of vertebrates is known to prey on adult anurans, including mammals, fishes, larger frogs, turtles, and snakes, and wading birds (Duellman and Trueb 1986; Wells 2007).

Several aspects of CRTO biology and behavior help individuals avoid, escape, or defend against predation, or help populations absorb losses from predation:

- As noted in chapters 1 and 2, their large body size may reduce predation on CRTO adults. However, CRTO adults do not achieve their full body size for 2 years or more, during which time they are presumably more vulnerable to predation.

- As also noted in chapters 1 and 2, their seasonal and nocturnal activity patterns as adults, high fecundity, breeding in isolated and sometimes strictly seasonal pools rather than permanent and sometimes flowing waters, and rapid maturation to the adults life stage may all help CRTO reduce or avoid predation or counter its demographic effects.

- As also noted in chapters 1 and 2, their toxic secretions as adults present a strong anti-predator defense, reinforced by distinct posturing and associated warning or threatening behaviors. As noted in chapter 2, the literature reviewed for this CEM indicates that bufonid larvae and metamorphs, and possibly also their eggs, may also produce toxic compounds. However, the literature does not indicate whether this is the case specifically for CRTO.

- The runoff that fills the seasonal pools preferred by CRTO as breeding sites may be turbid, at least initially, until the suspended sediment settles out (Cotten and Leavitt 2016). While present, the turbidity presumably could lower the visibility of CRTO eggs and larvae to sight-feeding predators, as it can to field investigators attempting to monitor CRTO breeding (Cotten and Leavitt 2016).

- CRTO adults limit the types of predators to which they are vulnerable by foraging only nocturnally and remaining inactive in their burrows for much of year. However, the latter behavior does not protect them from species that can dig up their prey, such as the American badger (*Taxidea taxus*) (see discussion of the adults life stage in chapter 2; see also chapter 4, "Vertebrate Community"). Hypothetically, their pattern of using burrows also may not protect them from predators that can move easily into burrows themselves, such as snakes. However, the literature reviewed for this CEM does not address the topic.

- Anuran larvae may exhibit specific behaviors in the presence of predators that reduce their vulnerability to predation (Alford 1999; Wells 2007). For example, tadpoles may aggregate, a safety-in-numbers strategy exhibited by American toads (*Bufo bufo*) (Arnold and Wassersug 1978; Watt et al. 1997). Arnold and Wassersug (1978) note,

  "During periods of anuran metamorphosis, garter snakes converge on the shoreline and their diets are biased towards transforming stages. This bias appears to reflect the locomotor ineptitude of metamorphosing anurans; transforming anurans can neither swim nor hop as effectively as pre-metamorphic tadpoles or post-metamorphic [adults], respectively…Metamorphic synchrony in certain anurans (Bufo) *may have evolved as a defense against predation during metamorphosis. This synchrony could satiate predators. Certain anurans (e.g.,* Bufo, Scaphiopus*) form post-metamorphic aggregations which may represent 'selfish herds' in which individuals gain protection by association with more vulnerable conspecifics."*

  Anuran larvae also may reduce their feeding activity and seek refuge when they sense a predator (Lawler 1989). The latter behavior, in turn, may result in smaller size at metamorphosis (Skelly and Werner 1990), which may adversely affect future survival and reproductive success (Berven 1990; Scott 1994). However, the literature reviewed for this CEM provides no information on such larval behaviors in relation to predation or their possible effects in CRTO.

The literature reviewed for this CEM provides only limited information on observed and possible predators of CRTO adults and only hints about possible predators of CRTO eggs or larvae and metamorphs. Chapter 4 (see "Arthropod Community" and "Vertebrate Community") summarizes information on arthropod and vertebrate species proposed or known to prey on CRTO, including species that appear to have learned or evolved ways to avoid or tolerate their toxic secretions.

RESTING/HIDING

All animals evolve resting and hiding behaviors for sleep and protection from predators and environmental stressors, including high and low daily and seasonal temperatures and extreme weather conditions. However, as noted above, this chapter, and chapter 2, the literature reviewed for this CEM provides no information on resting/hiding behaviors in CRTO larvae or metamorphs and only a little on such behaviors in CRTO adults.

Anuran larvae in general typically scatter when startled and, when not actively swimming or foraging, settle themselves to the bottom in shallow settings with very low flow and use benthic debris and crevices in the substrate as cover (Duellman and Trueb 1986). However, the subject apparently has not been studied in CRTO.

As noted above in the discussion of competition, this chapter, and in chapter 2, CRTO adults rest and hide in abandoned rodent burrows and similar shallow underground during the day from May through August and both day and night from September through April. As quoted above from Fouquette, Jr. et al. (2005), unpublished data from a study near Tucson found that body temperature in a CRTO adult in a burrow beneath a railroad track varied from 11.7 to 29.7 °C over the course of 264 days, a period that included both active and dormant seasons. This range of variation indicates that the burrow did not provide its occupant with significant thermal insulation.

The literature on CRTO discusses, but does not provide, systematic evidence for the physiological adaptations involved with CRTO dormancy during their inactive portion of the year nor information on whether this dormancy should be considered a form of aestivation, torpor, or other adaptation to risks of thermal stress or desiccation. The literature reviewed for this CEM also does not discuss how CRTO find, occupy, or retain possession of these underground refuges; what factors may affect refuge site selection among alternatives (e.g., soil type, moisture; proximity to other CRTO; etc.); or whether they ever excavate their own burrows or modify existing features to improve or sustain their habitability.

The literature reviewed for this CEM does not include any descriptions of hiding behavior among CRTO adults outside their burrows. Instead, as noted in the discussion of predation (see above, this chapter), they either do not react to the approach of other fauna or exhibit a repertoire of presumably defensive behaviors. These behaviors include facing the potential threat, inflating their bodies, and orienting their parotoid glands toward the threat while making a hissing sound.

THERMAL STRESS

Exposure to water or air temperatures outside their ranges of tolerance render anurans in every life stage vulnerable to reduced metabolic rates, reduced growth, impaired performance, disease, stress, and mortality (Wells 2007). Mann et al. (2009) summarize evidence for synergistic effects of thermal stress with disease and chemical stress, concluding 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."

Unfortunately, the literature on CRTO provides very little information on ranges of thermal tolerance for any life stage or the effects of temperature variation on egg, larval, metamorph, or adult growth. The literature reviewed for this CEM also does not provide data on sex ratios in hatched cohorts or among adults to assess for possible distortions due to exposure to temperature extremes.

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 biological activities and processes for one or more life stages.

This chapter identifies 10 habitat elements that may affect 1 or more critical biological activities or processes among the 3 CRTO life stages. Some of these habitat elements differ in their details among life stages. For example, different vertebrate species may prey on different life stages of CRTO. 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 CRTO conceptual ecological model includes habitat elements that species accounts and scientific studies identify as demonstrably or potentially directly affecting one or more critical biological activities or processes for one or more CRTO life stages or for similar or related species in similar habitats. Table 3 lists the 10 habitat elements included in the CRTO conceptual ecological model and the critical biological activities or processes that they may *directly* affect across all CRTO life stages. Habitat elements may also directly affect each other.

The authors of this CEM considered including an additional habitat element, substrate, to address the effects of variation in substrate texture (size composition) and stability on CRTO burrowing and breeding site selection. However, the literature reviewed for this CEM provides no information on soil affinities for CRTO burrow site selection. In turn, investigations of CRTO breeding site selection in the Bill Williams, Agua Fria, and Verde River valleys (Leavitt et al. 2017) and in Goldwater Range-East (Kiesow 2015; Kiesow and Griffis-Kyle 2017) found that differences in substrate did not affect which pools CRTO selected versus did not select as breeding sites. Therefore, the authors of this CEM determined that, while evidence in the future may support including such a habitat element, there is no need to do so now.

Except where noted, the sources for the following information are AmphibiaWeb (2019), which updates information from Fouquette, Jr. et al. (2005); LCR MSCP (2016); Nafis (2019); NatureServe (2019); Sullivan and Fernandez (1999); and , Thomson et al. (2016). These publications summarize all earlier studies. Where appropriate and accessible, those earlier studies are directly cited. Other key sources of information include the results of investigations of CRTO habitat in the Bill Williams, Agua Fria, and Verde River valleys (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a, 2016; Leavitt et al. 2017; Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b), and in Goldwater Range-East (Kiesow

Table 3.—CRTO 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 are proposed to directly affect which critical biological activities or processes [**X** = unidirectional; ***X*** = bi-directional].)

Affected critical biological activity or process ➔ / **🡻 Causal habitat element**	**Aggregation/dispersion**	**Breeding**	**Chemical stress**	**Competition**	**Disease**	**Foraging**	**Mechanical stress**	**Predation**	**Resting/hiding**	**Thermal stress**
Arthropod community				X		X		X		
Chemical contaminants		X	X							
Fire regime										X
Infectious agents					X					
Monitoring, capture, handling							X		***X***	
Periphyton & POM						X				
Temperature		X								X
Vegetation assemblage	X	X								
Vertebrate community				X		X		X		
Water availability	X	X	X				X			

2015; Kiesow and Griffis-Kyle 2017). In addition, where appropriate, the discussions of individual critical biological activities and processes draw upon literature concerning anurans in general. The results are hypotheses to make the best use of the available information.

The following paragraphs discuss the 10 habitat elements in alphabetical order. As with all such discussions 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 growth, survival, or fertility (Rosenfeld 2003; Rosenfeld and Hatfield 2006). The diagrams and other references to habitat elements in this document identify each habitat element by a one-to-three-word short name. Each short name in turn refers to a longer, full name. For example, “fire regime” is the short name for “The frequency, timing, spatial extent, and severity of fire in areas with existing or potential CRTO breeding and foraging habitat.” The following paragraphs provide both the short and full names for each habitat element and a detailed definition.

ARTHROPOD COMMUNITY

Full name: **The taxonomic composition, size range, spatial and temporal distributions, abundances, and activity levels of the arthropod community in and around existing or potential CRTO breeding and foraging habitat**. The arthropods of concern include species—including aquatic larvae—that may prey on CRTO eggs, compete with or prey on CRTO larvae or metamorphs, or compete with or serve as food items for CRTO adults. The types and abundances of arthropods available at night necessarily affect CRTO adult foraging success and nutrition.

There is a growing literature on the arthropod communities in the Lower Colorado River Valley (e.g., Anderson 2012; Andersen and Nelson 2013; Eckberg 2011, 2012; Nelson 2009; Nelson and Wydoski 2013; Nelson et al. 2015; Ohmart et al. 1988; Pratt and Wiesenborn 2009, 2011; Rubin et al. 2014; Trathnigg and Phillips 2015; Wiesenborn 2010, 2012, 2013, 2014a, 2014b; Wiesenborn et al. 2008). A full review of this literature is beyond the scope of this CEM; however, it should be noted that the edges of riparian vegetation near seasonal or permanent surface water may offer especially abundant insect populations for CRTO foraging as a result of aquatic insect productivity in these settings (Blakey et al. 2017; Hagen and Sabo 2012, 2014; Rubin et al. 2014).

Arthropod predation on anurans is well documented worldwide (Toledo et al. 2007). While the literature reviewed for this CEM does not address this topic specifically for CRTO, it does provide information relevant to the greater LCR ecosystem on possible arthropod predators in various developmental stages among amphibians in general.

- As noted in chapter 1, the non-native virile or northern crayfish is a particularly aggressive predator of Arizona native amphibian eggs and larvae (Fernandez and Rosen 1996). These findings are consistent with reports worldwide of crayfish as predators of amphibian eggs and larvae.

- Reported predators of the larvae and possibly also the eggs of native frogs that occur in the greater LCR ecosystem (AZGFD 2006; Sredl 2018) include several types of insects, notably giant water bugs (Belostomatids), backswimmers (Notonectids), predaceous diving beetles (Dytiscids), and the aquatic larvae (nymphs) of dragonflies (Anisopterans). However, these reports appear to rest on general knowledge of these taxa rather than observations of their feeding on native southwestern frogs in particular. The same literature also includes reports of the red swamp crayfish (*Procambarus clarkii*) as predators of frogs of all life stages.

However, as noted in chapter 2, CRTO larvae in isolated, seasonal pools may face fewer of these kinds of predators than CRTO larvae in permanent water bodies: CRTO metamorphose within a month of oviposition, and many arthropods may not be able to colonize isolated, seasonal pools or grow fast enough to pose a threat to the CRTO young in these settings in such a short time.

The aquatic larvae of some of the arthropods known to occur in the LCR ecosystem (see citations above) are herbivorous and, therefore, potentially could compete with CRTO larvae for food. Again, however, CRTO larvae in isolated, seasonal pools may face fewer of these kinds of competitors than CRTO larvae in permanent water bodies,

The northern crayfish not only preys on small aquatic vertebrates in the Southwestern United States, it also modifies habitat in ways that may affect amphibian use of such habitat. Specifically, this species of crayfish reduces aquatic macrophyte vegetation and the cover it can provide for amphibians in general (Fernandez and Rosen 1996; Rosen et al. 2013). While detrimental to some amphibians, however, such changes potentially could benefit CRTO, which preferentially breed in water bodies with lower vegetation cover (see below, this chapter, "Vegetation Assemblage").

As discussed in chapters 2 and 3 concerning foraging, CRTO adults are known to feed on numerous species of terrestrial arthropods, including "…beetles (Coleoptera); wasps, ants, and bees (Hymenoptera); termites (Isoptera); sun spiders (Solifugae); true bugs (Hemiptera); butterflies and moths (Lepidoptera); spiders, mites, and scorpions (Arachnida); grasshoppers, locusts, and crickets (Orthoptera), millipedes (Spirobolida); and centipedes (Scolopendromorpha)" (LCR MSCP 2016). CRTO may prey on species that are protected by sting mechanisms or defensive secretions (LCR MSCP 2016) or at least may try to prey on them (Bogan and Eppehimer 2017).

Arthropods that prey on other arthropods in CRTO non-breeding habitat may compete with adult CRTO for food resources. However, as noted above, a review of the potentially relevant literature and data on the arthropod communities along the Lower Colorado River Valley is beyond the scope of this CEM.

Finally, arthropods, particularly insects, can significantly affect vegetation dynamics in all ecosystems. The effects of the non-native northern tamarisk beetle (*Diorhabda carinulata*), on the non-native saltcedar (*Tamarix* spp.) along the Colorado River valley provide a particularly clear example. Saltcedar has invaded large portions of the Southwestern United States, forming extensive mono-specific woodlands across lowlands adjacent to permanent water. The literature reviewed for this CEM does not report any occurrences of CRTO in saltcedar woodlands, raising the possibility that CRTO avoid such vegetation (see below, this chapter, "Vegetation Assemblage"). Resource managers intentionally

released the northern tamarisk beetle in 2001 in the Upper Colorado River Basin as a biocontrol for saltcedar (Bean and Dudley 2018). The beetle has spread widely, including down the Colorado River valley into the LCR ecosystem, where it currently occurs as far south as the Imperial National Wildlife Refuge as of January 2019 (RiversEdge West 2019). Repeated defoliation by the beetle usually causes the canopy to die back within 1 to 4 years, and can cause individual plant death within 2 years or more, with overall mortality rates up to 40%, depending on the site (Bean and Dudley 2018). However, the literature reviewed for this CEM does not document whether CRTO occupy areas from which saltcedar has been removed.

Chemical Contaminants

Full name: **The types and concentrations of potentially harmful chemical contaminants present in existing or potential CRTO breeding and foraging habitat**. This habitat element addresses potentially harmful chemical substances or conditions that may occur in existing or potential CRTO habitat either naturally or because of current or prior human activities in or around—including upstream of—these locations. Harmful chemical substances or conditions may occur in existing or potential CRTO breeding and foraging habitat as a result of direct deposition in existing or potential CRTO habitat, chemical reactions and biological processes in the water, and/or transport in the air or water from adjacent areas, including upstream in watersheds. Theoretically, harmful chemical substances or conditions for CRTO could include, for example, air-borne or water-transported herbicides, pesticides, and fertilizers, and mineral salts from irrigated agriculture; industrial and residential chemical wastes; or outcomes of chemical reactions and biological processes in stagnant water, including the decomposition of organic matter. Chapter 5 discusses some possible sources of such contaminants.

The literature reviewed for this CEM does not present evidence of specific chemical contaminants causing harm to CRTO in any life stage, either in the LCR ecosystem or elsewhere. Consequently, the literature does not identify any specific chemical contaminants of potential concern for CRTO conservation. However, as noted in chapter 2 and in the discussion of chemical stress in chapter 3, the waters of the LCR have elevated salinity and selenium. Based on evidence of effects on other anurans, exposure to elevated salinity potentially is harmful to CRTO eggs and larvae, and exposure to elevated concentrations of selenium either in the water or in the diet potentially can harm all CRTO life stages.

As also noted in chapter 3 (see "Chemical Stress"), amphibians worldwide 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 in amphibian tissue (Bank et al. 2007; Blaustein et al. 2003; Brühl et al. 2013; Davidson et al. 2002; Mann et al. 2009; Smalling et al. 2015; Unrine et al. 2004; EPA 2016). However, the literature reviewed for this CEM does not address the effects of anthropogenic pollutants specifically on CRTO.

Chapter 3 (see "Chemical Stress") also notes that most observations of CRTO have focused on areas away from significant agricultural, industrial, or urban land use (i.e., away from areas where they may be exposed to elevated pollutant levels). However, CRTO in Arizona and southern California occur in several settings with known or likely elevated concentrations of chemical contaminants, which suggests that CRTO may tolerate elevated exposure to at least some contaminants:

- CRTO have been observed in agricultural areas, including in irrigation ditches fed by diversions from the LCR. As discussed in chapter 5 (see "Land Use"), commercial agricultural practices in the LCR valley involve a variety of chemical applications. On the other hand, Ronning (C. Ronning 2020, personal communication notes that "…the documented locations of CRTO on the Bill Williams and Big Sandy Rivers downstream of Wikieup, Arizona, do not have agriculture and, therefore, the threat of direct pesticide exposure is low at those locations." In fact, irrigated agriculture is not present anywhere in the Bill Williams-Big Sandy-Santa Maria River watershed above Alamo Lake.

- Numerous studies document water quality along the LCR, its off-channel environments, and the Bill Williams River (e.g., Arizona Department of Environmental Quality 2016a, 2016b, 2016c, 2018; Hinck et al. 2007, 2009; LCR MSCP 2004, 2018a; Ohmart et al. 1988; Patiño et al. 2012; Reclamation 2010, 2011a, 2011b; Seiler et al. 2003; Stolberg 2009, 2012; Tuttle and Orsak 2002). For example, the Bill Williams River immediately below Alamo Dam—the floodplain of which is known CRTO breeding habitat (Leavitt et al. 2017)—contains ammonia at concentrations recognized as harmful to fishes and other aquatic life (Arizona Department of Environmental Quality 2016a, 2016b, 2018). Exposure to ammonia can cause mortality in all amphibian life stages and also cause deformities in developing embryos (Mann et al. 2009). These effects of ammonia vary with water temperature (see below, this chapter).

- Investigations in Goldwater Range-East in 2012 found ammonia dissolved in high concentrations in isolated permanent and seasonal pools in CRTO habitat (Griffis-Kyle et al. 2019). However, CRTO did not appear to avoid these pools as breeding sites (Kiesow 2015; Kiesow and Griffis-Kyle 2017). This lack of avoidance could indicate that CRTO in this area breed in any water they can find regardless of its chemical quality or that they can tolerate or cannot detect elevated ammonia levels. The study in Goldwater Range-East did not investigate egg or larval development, or survival in the affected pools.

FIRE REGIME

Full name: **The frequency, timing, spatial extent, and severity of fire in areas with existing or potential CRTO breeding and foraging habitat**. Wildfires may occur naturally, although infrequently, in the native plant communities of the greater LCR ecosystem and may also occur through human causes (Conway et al. 2010; LCR MSCP 2013, 2018a; Meyer 2005; Stromberg et al. 2009). The LCR MSCP is authorized to use prescribed fire as a tool for habitat management (LCR MSCP 2018a).

CRTO occur in numerous native plant communities, from sparsely vegetated areas dominated by creosote bush and white bursage (*aka* burrobush) to mesquite (*Prosopis* spp.) and pine woodlands (see below, this chapter, "Vegetation Assemblage"). However, CRTO appear to occur in these plant communities only when those communities occur close to permanent or seasonal water. Susceptibility to wildfire varies widely among these diverse plant communities. Areas dominated by creosote bush and white bursage, for example, have only a low susceptibility to wildfire due to their sparse vegetation, including sparse herbaceous ground cover (except where invaded by non-native grasses) (Marshall 1994, 1995).

Theoretically, fire burning across a site occupied by CRTO could affect them in either of three ways:

1. A fire across a breeding site while eggs, larvae, or metamorphs are present could kill all aquatic life in the affected pool(s) (Whitney et al. 2015). Similarly, a fire across CRTO non-breeding habitat could kill CRTO adults if the fire catches them outside their burrows or if their burrows do not provide sufficient protection. However, the literature reviewed for this CEM provides no information on the direct effects of any wildfires on CRTO.

2. Fire burning across CRTO non-breeding habitat could alter the arthropod community in the area and alter the spectrum of vertebrates that occupy or visit the area either directly by killing the fauna or indirectly by altering the vegetation. However, the literature reviewed for this CEM similarly provides no specific information on the effects of wildfires on the arthropods and vertebrates that affect CRTO.

3. Upland wildfire in watersheds in which CRTO occur could indirectly alter breeding site habitat. Parker (2006) describes how upland fires in some watersheds in the Rincon Mountains in Saguaro National Park above Tucson, Arizona, resulted in increased soil erosion from these watersheds. This erosion, in turn, resulted in the filling of former pools with sediment along the downstream waterways, which in turn resulted in local extirpations of the lowland leopard frog. CRTO use of seasonal pools along such waterways presumably would make them vulnerable to such causal chains as well.

INFECTIOUS AGENTS

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

The literature reviewed for this CEM provides very little information on possible infectious agents in CRTO. As noted in chapter 2, the literature reports the presence of a handful of parasites in CRTO but provides no information on their effects among CRTO in the wild. The literature also includes no reports on occurrences—let alone impacts—of the increasingly widespread and devastating amphibian disease, chytridiomycosis (*aka* chytrid fungal disease), or its agent, *Batrachochytrium dendrobatidis* (*aka Bd*), in CRTO. However, this absence of reports may reflect an absence of investigations rather than a lack of occurrences of the illness. The literature reviewed for this CEM simply does mention any efforts to assess *Bd* occurrence in CRTO in the wild. On the other hand, two lines of evidence suggest that CRTO may not be highly susceptible to *Bd*. As noted in chapter 2, Helmick et al. (2018) found no evidence of exposure to chytrid fungus in five captive-reared CRTO. Further, CRTO in the wild do occur in localities where other anurans are known to be infected with *Bd* (Rosen and Caldwell 2004), with no reports of illness among the CRTO present.

MONITORING, CAPTURE, HANDLING

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

Following a pilot study in 2011–13 (Cotten and Leavitt 2014a), the AZGFD conducted field trials in 2014 and 2015 to evaluate the relative effectiveness of five survey methods to assess presence/absence of CRTO during the breeding season along the Bill Williams River valley (Miller and Cotten 2016; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b): (1) visual encounter surveys (VESs) , (2) VESs with an audio broadcast call/response component (VES C/Rs), (3) funnel trap arrays (FTAs), (4) environmental deoxyribonucleic acid (eDNA) analysis of water samples, and (5) digital automated recorder (DARs) recordings. Sample sizes for the different methods were constrained by the absence of CRTO breeding in the Bill Williams River valley in 2015 (see above, chapter 3, "Breeding"). The investigations did not evaluate methods for surveying CRTO outside the breeding season. The investigations summarized the findings as follows (O'Donnell and Leavitt 2017b):

> *"In 2014, Colorado River toads were detected 11 times with VESs, 7 times with VES C/R broadcast calls, 0 times with FTAs, and 80 times with DARs. In 2015, Colorado River toads were detected six times with VESs, and they were not detected with any other method. eDNA was a very effective method for detecting this species when water was present (toad deoxyribonucleic acid [DNA] was detected in 10 of 11 samples), but only 3 sites in 1 year had enough water to conduct eDNA sampling.*

It is useful to quote in full the conclusions of these investigations after statistical analysis (O'Donnell and Leavitt 2017b):

> *"For Colorado River toads, VES C/Rs and DARs were the most cost-efficient methods of detection. A VES is still the preferred method when rain is not predicted and surveys must be conducted regardless of the weather because VES C/Rs and DARs are only suitable at detecting Colorado River toads after a monsoon event. When surveys can be conducted during or shortly after a rain event, VES C/Rs are likely to be effective, although they have high labor costs and require larger crews spending longer time conducting surveys. DARs have the added benefit of requiring very little labor, and thus are very cost effective once the recording devices have been purchased. They do require at least some*

significant rain during a season to be effective, and in some years they may fail to detect a species even when it is present if there is insufficient rain to prompt a breeding event.

Surveys (VESs) of Colorado River toads in the Bill Williams River from 2011 through 2013 found no breeding behavior, with the exception of one male that had fresh egg mass strands on its back (Cotten and Leavitt 2014). The use of only DARs and VES C/Rs could have missed this simply because there was no calling detected by biologists for this breeding event. VESs can provide the identification of potential or current breeding sites and associated activity such as amplexus, egg masses, or tadpole success as well as general activity not associated with breeding behavior such as foraging. The drawback of this method is that it is costly in terms of time and labor. DARs and VES C/Rs lack the ability to detect foraging adults or potential breeding locations. If setting DARs in a new study site, one must place the devices near areas where water will later pool.

"DARs have a high upfront cost, which contributes to their lower overall CCDI [cost-corrected detection index]. *However, over a multi-year span their effective cost will decrease while other methods will remain relatively constant. Therefore, they become more cost efficient and have a higher CCDI over time compared to the other methods tested, making them a very valuable tool for long-term monitoring.*

Since DARs have the capability to record a large amount of audio recordings, they can be left onsite for extended periods of time. The recorders were checked and the data storage cards replaced approximately every 3 weeks. However, to further reduce overall cost of DARs, one could limit the removal of data storage cards to once or twice a season and therefore lessen the travel time to the study site (doing so increases the risk of losing more data from equipment loss or failure, however.) All other methods require personnel to be onsite to record data, which includes a greater amount of travel and thus increases costs.

The one-season trial implementation of DARs in the Swansea Wilderness of the Bill Williams River…demonstrated that this is an effective and efficient method for monitoring the presence of Colorado River toads. The best model indicated that the detection probability varied by week, with detection probability estimates of 0 for most weeks but ranging from 0.2 to 0.7 in weeks 4–6 of this study (August 3–23, 2016). This again emphasizes the importance of correct timing and a reliance on unpredictable monsoon rains in detecting this species. The efficiency of this method could be further increased by analyzing only recordings from periods when rain occurred."

O'Donnell and Leavitt (2017a; see also Miller and Cotten 2016) elsewhere also 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." Kiesow (2015) and Kiesow and Griffis-Kyle (2017) used DARs to assess CRTO breeding activity in Goldwater Range-East in 2010 and 2012.

These conclusions of the AZGFD study of monitoring methods point to several biases that could arise in surveys of CRTO during the breeding season. CRTO do not always call—or not all CRTO males may call—during breeding (see also chapter 3, "Breeding"). Detection data from DARs and VES C/Rs thus can underestimate CRTO male densities. The investigators note that separate VESs carried out over the same periods monitored by VES C/R or DAR can detect CRTO even when they do not call. VESs at breeding sites also can occur during the daytime. However, investigators can encounter great difficulty when trying to conduct VESs for amphibians in dense vegetation, particularly in stands of saltcedar. Howland et al. (1997) found that lower densities of vegetation—both herbaceous and woody—enhance the visibility of native frogs for VES detections in Arizona, while higher densities impair it. Sredl et al. (1997a) had to abandon VESs altogether at one site in a mark-recapture study of lowland leopard frogs because of a substantial increase in vegetation density. Similarly, the AZGFD investigations along the LCR and Bill Williams River valleys (Cotten and Grandmaison 2013; Cotten and Leavitt 2014a, 2014b; Miller and Leavitt 2015; O'Donnell and Leavitt 2017a, 2017b) have consistently reported that high densities of woody vegetation—particularly saltcedar—greatly impair the effectiveness of VESs in the Bill Williams River valley.

One monitoring method could help assess CRTO activity within vegetation stands too dense for other methods or allow routine assessment of spatially extensive CRTO nocturnal activity in non-breeding habitat. As described by Fouquette, Jr. et al. (2005), an unpublished study successfully radio-tracked an adult CRTO for 264 days in the Tucson Mountains, Pima County, Arizona. However, NatureServe (2019) notes that most studies of toad activity patterns do not employed radio telemetry. Cotten (2011) proposed using radio-telemetry to assess habitat use for both CRTO and the lowland leopard frog "…should a stable population of either target species be encountered."

Camera traps also might help monitor CRTO nocturnal activity in non-breeding habitat and during the breeding season. Such traps could help assess breeding in the absence of calling activity (see chapter 3, "Breeding"). However, the literature reviewed for this CEM contains only one mention of CRTO documented by camera traps: Gutiérrez-González et al. (2016) report that such traps in 2012 and 2013 captured three nighttime images of mammals interacting with CRTO in the Northern Jaguar Reserve, Sonora, Mexico. The traps were deployed for general documentation of wildlife, not specifically to study CRTO.

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). However, the literature reviewed for this CEM does not discuss any sensitivities of CRTO to monitoring, capture, or handling.

Chapter 2 (see "Colorado River Toad Life Stage 3 – Adults") discussed the attention CRTO adults have received due to the hallucinogenic properties of its toxic secretions. As noted in that discussion, practitioners of alternative medicine have also looked into these secretions as possible tools in the treatment of, for example, addictions (Gutiérrez-González et al. 2016; Uthaug et al. 2019). However, the extent of private collecting for these purposes is unknown. Numerous websites also attest to interest in the selling and keeping of CRTO as exotic pets. However, again, the extent of private collecting for these additional purposes is unknown. Unsuccessful efforts to collect CRTO privately or the release of privately collected CRTO after attempts to keep them or collect their secretions presumably can cause mechanical stress (see chapter 3, "Mechanical Stress"). Hypothetically, the capture of CRTO to keep or sell as exotic pets would affect CRTO abundance similarly to successful predation. However, no information is available to consider the latter possible causal relationship.

PERIPHYTON & PARTICULATE ORGANIC MATTER

Full name: **The taxonomic composition, size, density, and nutritional quality of the periphyton and particulate organic matter in existing and potential CRTO breeding habitat.** This habitat element focuses on two broad classes of aquatic life and organic matter in CRTO breeding habitat: (1) the periphyton living on the mineral substrates, submerged plant parts, and submerged coarse plant litter in these waters and (2) the particulate organic matter (POM) in the water column and lying on 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 the water body or dropped and/or washed in from its margins and upstream.

As discussed in chapter 2 and also in chapter 3, (see "Foraging"), the literature reviewed for this CEM provides no specific evidence concerning the CRTO larval diet; however, CRTO larvae are assumed to be algivorous or omnivorous, based on larval diets in related species (Fouquette, Jr. et al. 2005). Unfortunately, the

literature reviewed for this CEM does not provide information on the types of periphyton or POM that may occur in water bodies where CRTO breed, and a literature review on this topic is beyond the scope of this CEM.

The autochthonous production of periphyton and POM contributes significantly to, and sometimes dominates, primary productivity in freshwater ecosystems. Autochthonous production 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). Hypothetically, therefore, autochthonous productivity might be low initially in a seasonal pool where CRTO may breed, immediately after the pool fills, because the water in the pool initially may be turbid (see discussions of "Breeding," "Competition," and "Predation" in chapter 3). However, depending on how quickly the turbidity disappears (as the suspended sediment settles), improved water clarity may quickly support autochthonous production. In the interim, again hypothetically, CRTO larvae may feed more on POM washed into the water during filling of each pool.

Autochthonous production in isolated pools affects the concentration of dissolved oxygen in the water and its variation through the day, and it can affect the pH of the water and reduce water clarity. Decomposition of new and existing dead organic matter, conversely, can alter the chemistry in isolated pools in ways that, for example, lower oxygen levels and release ammonia.

Hamilton (2003, 2004), Presser and Luoma (2006), the EPA (2016), and others note that selenium in freshwater ecosystems cycles through multiple ecological compartments. These compartments include not only surface and groundwater but also periphyton, other living POM, and dead POM in the substrate. 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. However, no study has specifically examined the ways in which these interactions could affect the possibility of selenium bioaccumulation in CRTO larvae.

Finally, other habitat elements may affect the availability of periphyton and POM in CRTO breeding habitat. Axelsson et al. (1997) found that grazing by crayfish can reduce the quantity and quality of periphyton and larger algae available as food and cover for amphibian larvae. Such competition from crayfish would compound the effects of their predation on amphibian larvae. Further, as noted above, this chapter (see "Arthropod Community"), studies in the Southwestern United States show that the northern crayfish reduces aquatic macrophyte vegetation and the cover it can provide for amphibians in general (Fernandez and Rosen 1996; Rosen et al. 2013). However, as also noted above, such reductions might benefit CRTO, which preferentially breed in water bodies with lower vegetation cover (see below, this chapter, "Vegetation Assemblage").

TEMPERATURE

Full name: **The air and water temperatures and their variation over time in existing or potential CRTO breeding and foraging habitat**. Water temperature and its variation—including the timing, magnitude, frequency, and duration of temperature extremes—can affect survival, growth, and vulnerability to other stresses during aquatic and semiaquatic life stages among amphibians in general (Duellman and Trueb 1986). Similarly, air temperature and its variation—again including the timing, magnitude, frequency, and duration of temperature extremes—also can affect daily and seasonal activity patterns, survival, growth, and vulnerability to other stresses during amphibian terrestrial life stages (Duellman and Trueb 1986). Unfortunately, the literature reviewed for this CEM provides very little information on thermal affinities or tolerances of CRTO in any life stage and no information on effects of temperature variation on survival, growth, or vulnerability to other stresses.

Anecdotal information indicates that CRTO adults are inactive and remain in their burrows in both cold and hot, dry weather but without quantitative data on what temperatures trigger such behavior (NatureServe 2019). As noted in chapter 3 (see "Breeding"), Kiesow (2015) found that CRTO attempted to breed in Goldwater Range-East in 2012 within 5 nights following a rainfall event in the vicinity of an individual pool only when two other conditions were also obtained: (1) the nighttime air temperature stood between 23 and 27 °C and (2) the concurrent relative humidity stood between 65 and 100% (see below, this chapter, "Water Availability").[6] Kiesow (2015) also notes, comparing the three species found together at breeding sites in Goldwater Range-East in 2012,

> *"Generally, a minimum* [air] *temperature of 18 °C is required for desert anurans to become active in the field with slightly higher temperatures required to initiate breeding activity (Tevis, 1966).* Anaxyrus punctatus *seem to have a wider tolerance of air temperature, ranging from 14 – 29.5 °C (mean: 21.7 °C), as compared to* S. couchii, *which ranges from 20 – 25 °C (mean: 23.5 °C) (Brattstrom, 1963). The critical temperature maximum for* A. punctatus *has been reported as 42.5 ± 2.3 °C (Rausch et al., 2008). There is less information about the*

[6] Griffis-Kyle et al. (2019) report that "during the summer 2012 the area received 65 mm of precipitation from July through October (100% of that year's rainfall) and averaged 33.1 °C (average maximum during same period 45.6 °C)," but no publications on the investigations provide air temperature data for individual CRTO breeding events. Similarly, Griffis-Kyle et al. (2019) report that summer water temperatures at five tinajas in 2012 averaged 26.5 °C (SE = 0.8), with average maxima of 42.6 °C (SE = 2.7), and at three artificial catchments averaged 26.8 °C (SE = 0.7), with average maxima of 35.1 °C (SE = 2.7), but no publications on the investigations provide water temperature data for individual CRTO breeding events.

> *thermal requirements and critical temperature maximum of* I. alvarius*; however, Brattstrom (1963) reports a mean body temperature measured in two individuals of 21.2 °C, slightly lower than the other two species."*

Otherwise, the only mention of effects of temperature on CRTO comes from studies of their mating calls. LCR MSCP (2016) notes that,

> *"The frequency or duration of advertisement or release calls is not related to body size or body temperature of individuals (Sullivan and Malmos 1994). The pulse rate of advertisement calls increases as the body temperatures of individuals increase (Sullivan and Malmos 1994). The pulse rate of release calls decreases as the body temperatures of individuals increase (Sullivan and Malmos 1994)."*

On the other hand, Leavitt et al. (2017) report no statistical difference in water temperature between pools used versus not used by CRTO as breeding sites in the Bill Williams, Agua Fria, and Verde River valleys in 2014. CRTO adults also appear able to survive wide variation in body temperature. As noted in chapter 3 (see "Resting/Hiding"), an unpublished study of an adult CRTO over 264 days in 1988 and 1989 found that the body temperature of the individual ranged from 11.7 to 29.7 °C.

VEGETATION ASSEMBLAGE

Full name: **The taxonomic composition, density, variability, and spatial and temporal structure of the vegetation assemblages in and surrounding CRTO breeding habitat and across CRTO non-breeding habitat**. This habitat element addresses woody, shrub, and herbaceous vegetation in the canopy, understory, and ground cover in these habitat settings (see the "Definitions" section immediately following the acronyms and abbreviations at the beginning of this document).

The literature reviewed for this CEM provides only limited information on the vegetation in areas occupied by CRTO adults as non-breeding habitat. The LCR MSCP (2016) summarizes this information as follows:

> *"Colorado River toads are semiaquatic toads that occur primarily in desert habitat, including mesquite-creosote lowlands, but also inhabit arid grasslands, oak-woodland habitat, riparian areas, and pine-oak-juniper forest (Fouquette 1970; Holycross et al. 1999; Stebbins 1985)… Holycross et al. (1999) observed this species in pine-oak woodlands, characterized by high densities of Chihuahua pine (*Pinus leiophylla*), Mexican pinyon (*Pinus cembroides*), alligator juniper (*Juniperus

> deppeana*), various oaks (*Quercus spp.*), and a native grassland in Chihuahuan desert scrub. Cole (1962) observed this species associated with agave (*Agave spp.*), joint fir (*Ephedra spp.*), mesquite* (Prosopis spp.), *Russian thistle (*Salsola spp.), *yucca (*Yucca spp.), *snakeweed (*Gutierrezia spp.*), and grasses. This species may have also expanded its range to agricultural areas when large-scale conversion of native habitat to agriculture took place."*

Fouquette, Jr. et al. (2005) additionally mention "rocky riparian zones with sycamore and cottonwoods" as CRTO non-breeding (foraging) habitat. Cotten and Leavitt (2014a) provide a more detailed description of CRTO non-breeding habitat along the Bill Williams River valley as follows:

> *"Colorado River toads …were located primarily in open, sandy desert habitat with little vegetation. Shrubs were the largest vegetation layers measured from the habitat points; this was the case due to toads often being observed sitting and foraging under creosote (*Larrea tridentate*) bushes on desert flats. Other than creosote, most of the vegetation measured in each plot was sporadic small clumps of grasses and forbs, with the area predominantly open sand. Sand has been the substrate variable in all toad locations, likely due to toads using mammal burrows in the sand as refuges during the day and cooler months (Lowe, personal observation)."*

AZGFD investigations in the Bill Williams River valley subsequent to the work of Cotten and Leavitt (2014a, 2014b) found that CRTO non-breeding habitat consisted of sandy features dominated by creosote bush, white bursage (*aka* burrobush), and desert salt bush (O'Donnell and Leavitt 2017a, 2017b). CRTO adults (when not breeding) thus do not consistently occur in association with any single type of vegetation assemblage. The common denominator in CRTO non-breeding habitat instead appears to be not their vegetation type but rather their proximity to permanent or seasonal surface water. The vegetation that occurs in such settings presumably varies with elevation, hydrology, topography, soil type, and other environmental factors.

However, the descriptions of CRTO non-breeding habitat do suggest two consistencies in their vegetation:

1. The vegetation in CRTO non-breeding habitat occupancy appears to consist mostly of types that provide very sparse canopy cover. Creosote bush and burrobush, for example, do not form dense stands but rather grow scattered across the land with large areas of open space (Marshall 1994, 1995). However, in the literature reviewed for this CEM, only the AZGFD studies along the Bill Williams River (O'Donnell and Leavitt 2017a, 2017b) provide even qualitative information on the spatial structure of the vegetation in which CRTO occur.

2. The literature does not report CRTO occupancy in stands of saltcedar, a vegetation type that occurs only in proximity to permanent or seasonal surface water (Zouhar 2003). Saltcedar in fact excludes native vegetation, resulting in sometimes extensive, pure stands of the invasive species. The literature reviewed for this CEM does not explicitly note this negative association of CRTO and saltcedar, let alone identify possible reasons for it such as canopy or stem density, food availability, or other possible factors. It is possible that the apparent negative association is simply an artifact of the history of investigations. As noted above (see this chapter, "Monitoring, Capture, Handling"), investigators encounter great difficulty when trying to conduct visual surveys for amphibians in stands of saltcedar (e.g., Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a; O'Donnell and Leavitt 2017a, 2017b). However, if the apparent negative association is not a result of sampling bias, then hypothetically, removal of saltcedar stands could affect the availability of CRTO non-breeding habitat.

The literature reviewed for this CEM also provides only limited information on the vegetation in and around CRTO breeding habitat. This information comes from surveys of pools used by CRTO as breeding sites, and nearby pools that were not used, in the Bill Williams, Agua Fria, and Verde River valleys in Arizona in 2014 and 2015 (Cotten and Leavitt 2016; Leavitt et al. 2017). Once the surveyors identified a pool being used by CRTO as breeding habitat, they randomly selected a "non-site" nearby within 50 m and collected data on several characteristics of both the breeding sites and non-sites as follows (Leavitt et al. 2017):

> "*If individual oviposition sites were attached to vegetation, the species of plants were identified using available taxonomic keys. In addition, the following variables were measured* [at oviposition sites]*:*
>
> - *Dimensions (height, length, and width) of the egg mass (millimeters)*
> - *Depth of the egg mass from the surface of the water to the top of the mass (centimeters [cm])*
> - *Distance from the bottom of the water to the underside of the egg mass (cm)*
> - *Percent canopy cover for each plant species directly over the egg mass*
> - *Distance to dense cover (cm)*
> - *Distance to crawl [defined as the distance required to reach an area from which an individual could escape out of water] (cm)*

- *Substrate at the bottom of the water column directly below the egg mass*
- *Water flow (recorded with a "yes" or "no" depending on the continuity of the flow)*
- *Water temperature (degrees Celsius)*
- *Water pH (recorded using a digital pH meter)*
- *Depth of the water column near the egg mass, measuring from the surface to the substrate at the bottom (cm)"*

Habitat variables measured at a randomly selected non-site location included:

- *Distance to dense cover*
- *Distance to crawl*
- *Substrate at the bottom of the water column*
- *Water flow*
- *Temperature*
- *Water pH*
- *Depth of the water column"*

The surveys did not record information on living vegetation in or immediately surrounding CRTO breeding sites versus non-sites unless the breeding CRTO attached their egg masses to vegetation.

Unfortunately, the surveys in these three river valleys found only 14 breeding sites in 2014, in the Bill Williams and Agua Fria River valleys but not in the Verde River valley; and no CRTO breeding sites in any of the three valleys in 2015 (see chapter 3, "Breeding"). The investigators could not carry out statistical comparisons between the site and non-site data due to the small sample size. Analyses of the breeding site data on their own indicated that (as also partially quoted in the discussion of breeding in chapter 3),

> *"Colorado River toads select shallow water with no canopy cover for oviposition. … Site descriptions from 2014 suggest that very little selection occurs at the site level; rather, it is at a much larger scale that Colorado River toads are selecting breeding habitat (Cotten and Leavitt 2016). They breed in open canopy water sources that are ephemeral in nature; therefore, any data related to water column depth or pH should be considered as transient variables that do not represent the moment of oviposition."*

The investigators also note that, among the 14 egg masses observed in 2014, 10 were attached to unknown materials, 3 to twigs of unknown species, and 1 to a mesquite branch.

VERTEBRATE COMMUNITY

***Full name*: The taxonomic composition, size range, spatial and temporal distributions, abundances, and activity levels of the vertebrate community in and around existing or potential CRTO breeding and foraging habitat**. This habitat element concerns the mammals, birds, reptiles, amphibians, and fishes that may prey on, compete with, or shape the habitat of CRTO in any or all life stages.

The literature reviewed for this CEM discusses vertebrate predation only on CRTO adults and then mostly focuses on CRTO toxic secretions and their effects on would-be predators. As noted in chapter 2, the literature reviewed for this CEM does not discuss whether CRTO eggs, larvae, or metamorphs are also capable of secreting toxins or whether CRTO toxicity varies with other factors. However, as noted in chapter 2, it is possible that bufonid eggs, larvae, and metamorphs also contain toxins (Hayes 1989).

As noted in chapter 2, Gutiérrez-González et al. (2016) report several nocturnal instances in which mammalian potential predators were observed to approach and then move away from CRTO adults. These instances are at least anecdotal evidence that potential predators learn to avoid attacking CRTO adults. However, as summarized by Gutiérrez-González et al. (2016) from the literature and new observations, at least a few vertebrates have found ways to prey on CRTO adults either by avoiding or tolerating their secretions. These vertebrates include raccoons (*Procyon lutor*), American badgers, black-necked gartersnakes (*Thamnophis cyrtopsis*), and a Central American indigo snakes (*Drymarchon melanurus*). The first two of these four species occur throughout the CRTO range, including in the greater LCR ecosystem; the third occurs across the CRTO range elsewhere in Arizona; and the last occurs across the CRTO range only in Mexico.

Gutiérrez-González et al. (2016) review early reports of raccoons consuming CRTO adults by flipping them over on their backs and attacking their torsos, thereby avoiding the dorsal glands that secrete the toxins. A camera trap monitored by Gutiérrez-González et al. (2016) in the Northern Jaguar Reserve, Sonora, Mexico, recorded a badger carrying a large adult CRTO in its mouth in the middle of a January night. The toad would have been dormant in a burrow at that time of year, but badgers forage in part by digging up their prey. The

investigators were not able to determine how the badger was able to tolerate the CRTO toxins or how it consumed its prey. Gutiérrez-González et al. (2016) further note,

> *"Enderson and Bezy (2002) reported Sonoran Desert Toads in the diet of the Black-necked Garter snake (*Thamnophis cyrtopsis*), including an individual at Buenos Aires National Wildlife Refuge, Arizona, that contained 14 small Sonoran Desert Toads. Villa et al. (2015) found a Central American Indigo Snake (*Drymarchon melanurus*) consuming a Sonoran Desert Toad on the Río Sonora, Sonora. Additionally, JCR* [James C. Rorabaugh, a co-author] *once observed a captive Mexican Hog-nosed Snake (*Heterodon kennerlyi*) attempting to consume a juvenile Sonoran Desert Toad. However, when the toad was about half-way into the snake's mouth, the snake began to foam at the mouth, exhibited righting difficulties, and subsequently spit the toad out. The snake was incapacitated for a short while, but it recovered."*

Finally, Gutiérrez-González et al. (2016) list previous suggestions that "…skunks (*Mephitis* sp.), ringtails (*Bassariscus astutus*), coatis (*Nasua narica*), bobcats (*Lynx rufus*), gray foxes (*Urocyon cinereoargenteus*), and other mammalian predators may also have learned how to safely prey upon these toads." Presumably, coyotes (*Canis latrans*) also belong on this list. All of these species hunt at night. Additionally, all of the mammals and reptiles known or suggested as possible predators of CRTO adults could also compete with them for other food items. On the other hand, all these species are native to the region, and CRTO therefore likely co-evolved with them in ways that reduce competition or compensate for its effects.

Ravens (*Corvus corax*) systematically kill and eviscerate toxic adult western toads (*Bufo boreas*) at breeding aggregations in Oregon (Olson 1989). Ravens also occur throughout the CRTO range. However, as with the mammals suggested as additional possible predators of CRTO adults, the literature reviewed for this CEM does not provide evidence that ravens do in fact prey on CRTO. On the other hand, corvids (ravens and crows) elsewhere also have learned how to kill and consume other toxic toads, suggesting that this may be a general ability. Starr (2018) reports that Australian crows (*Corvus orru*) have learned how to kill and consume cane toads (*Rhinella marina*), a large and highly toxic species introduced to Australia in 1935. The crows flip the cane toads over and eviscerate them—the same method developed by raccoons for consuming CRTO and by ravens for consuming western toads in Oregon.

The general literature on amphibians recognizes wading birds such as bitterns and herons, and small mammals as potential predators of younger and smaller amphibians (Duellman and Trueb 1986; Wells 2007). As noted in chapter 2, the greater LCR ecosystem is home to other vertebrates that potentially could prey

on CRTO eggs, larvae, or metamorphs. These include the northern Mexican gartersnake, American bullfrog, Rio Grande leopard frog, tiger salamanders, mud turtles, great blue herons, Yuma clapper rail, and least bittern. However, the literature does not indicate whether any of these vertebrates in fact do prey on CRTO eggs, larvae, or metamorphs; whether CRTO eggs, larvae, or metamorphs contain any of the toxins that help CRTO adults discourage predation; or whether any of these vertebrates have learned ways to avoid or tolerate such toxins.

Fishes presumably also may prey on CRTO eggs, larvae, or metamorphs in the water, or even on CRTO adults when they aggregate at breeding sites. However, the literature reviewed for this CEM does not address the possibility. Temporary (seasonal) pools used by CRTO as breeding sites may contain few fishes. Further, the literature reviewed for this CEM does not address the extent of CRTO use of permanent water bodies, where fishes may be more likely to occur. For these reasons, this CEM does not provide suggestions for fish species that could prey on CRTO in any life stage.

At least two other native mammals, beavers (*Castor canadensis*) and muskrats (*Ondatra zibethicus*), conceivably may affect CRTO 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 where they increasingly shape 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 CRTO have not been investigated but conceivably could be both beneficial and detrimental. Ponds behind beaver dams create permanent water bodies but potentially could inundate areas where seasonal pools once formed. Cotten and Grandmaison (2013) state that 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." 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 visual surveys for amphibians. Rosen et al. (2013) similarly caution that the pools created by beaver in wetland areas can favor the growth of non-native plants. On the other hand, both beavers and muskrats eat aquatic macrophytes and, thereby, may create the kinds of more open shallows that CRTO appear to prefer as breeding sites (see chapter 3, "Breeding" and above, this chapter, "Vegetation Community").

Finally, the possible effects of native mule deer (*Odocoileus hemionus*) and non-native cattle and burros (*Equus asinus*) on CRTO also are not clear. Grazing cattle and burros conceivably could trample CRTO breeding sites. Further, their movement patterns could make such sites more accessible to other large vertebrates, including people. Ronning (C. Ronning 2020, personal communication) notes that "Burros can create paths to pools and riverine areas which help other wildlife access these areas when native vegetation and tamarisk are thick." On the other hand, their grazing in the Southwestern United States can sustain more open vegetation by reducing the density of the understory and preventing the establishment of cottonwood (*Populus* spp.) and willow (*Salix* spp.) seedlings (Kauffman et al. 1997). Jaeger and Rivera (2017) observed that "…cattle activity appears to have limited the density of cattails located in the main pool" at Quail Spring, Nevada, affecting habitat quality there for relict leopard frogs (*Rana onca = Lithobates onca*). Krueper (1993) and Krueper et al. (2003) report that fencing cattle out of riparian habitats in the San Pedro Riparian National Conservation Area in southeastern Arizona resulted in an increased density of native riparian vegetation. However, no studies have been conducted to explicitly examine the impacts of cattle or burro activity on CRTO site use or behaviors.

WATER AVAILABILITY

Full name: **The timing, magnitude, and duration of elevated humidity, rainfall, runoff, and surface water availability in and around existing or potential CRTO breeding habitat**. This habitat element addresses features of the hydrologic regime that may affect CRTO breeding activity and success at individual sites, including (1) humidity and rainfall during the breeding season and (2) surface water permanence, depth, and movement (flow or turnover), and their temporal variability, including extreme events (droughts and floods). The following paragraphs discuss each of these two sets of features in turn.

As discussed above (see chapter 2 and also chapter 3, "Aggregation/Dispersion" and "Breeding"), the presence/absence and timing of CRTO breeding activity at individual sites depend on the interplay of at least three features of the weather during the warmest months of the year:

- Rainfall in the vicinity greater than 25 mm in a single 24-hour period (Sullivan and Fernandez 1999). If the rainfall is too heavy (e.g., greater than 75 mm over a 24-hour period) and causes local flooding, the toads may wait 2 or 3 days for the water to subside into still pools before they gather (Fouquette, Jr. et al. 2005). The literature reviewed for this CEM does not indicate how close spatially the rainfall needs to occur to the water body to trigger breeding.

- Nighttime air temperature between 23 and 27 °C (Kiesow 2015; Kiesow and Griffis-Kyle 2017).

- Nighttime relative humidity between 65 and 100% (Kiesow 2015; Kiesow and Griffis-Kyle 2017).

CRTO also may gather to breed at permanent water bodies before monsoonal rains begin in an area, although the triggers for such activity have not been studied. CRTO may not breed at all in dry or dry-cool years even when permanent water is available (Leavitt and O'Donnell 2017a, 2017b; Leavitt et al. 2017; Miller and Cotten 2016; Sullivan and Fernandez 1999). The study in Goldwater Range-East reported by Kiesow (2015) and Kiesow and Griffis-Kyle (2017) recorded CRTO breeding only in the summer of 2012 but had attempted and failed to record CRTO breeding in the summer of 2010, a cooler, dryer summer (see also Griffis-Kyle et al. 2019). This variability in whether, when, and where CRTO breed has not been systematically studied.

CRTO use of temporary, seasonal pools as breeding sites under relatively natural conditions depends on the timing, duration, and cumulative magnitude of rainfall. Rainfall may accumulate to form pools in low spots away from drainage channels, or it may accumulate as runoff that fills pools in seasonal drainage channels and backwaters. Pools in seasonal drainage channels and backwaters in the Southwestern United States may fill low spots in the deposited sediments or pockets in the bedrock created by stream erosion below small waterfalls, also known as tinajas or plunge pools (Kiesow 2015; Levick et al. 2008). The duration of such seasonal pools depends on air temperatures and insolation; pools shaded by canopy vegetation or canyon walls may persist longer than pools without any shade. However, as noted above, this chapter (see "Vegetation Assemblage") and chapter 3 (see "Breeding), CRTO appear select breeding pools with little vegetation cover. Pools need only persist (presumably with suitable water quality) for approximately a month for CRTO to develop from embryo through metamorphosis.

CRTO also may breed in pools created by artificial releases from water management structures. Cotten and Leavitt (2016) note that,

> *"The low flows of the BWR [Bill Williams River] from Alamo Dam may also contribute to a lack of breeding habitat (Cotten and Leavitt 2014). Higher flows in the BWR may create more isolated pools adjacent to the river after monsoon floods suitable for breeding."*

The literature reviewed for this CEM does not report CRTO breeding in strongly flowing water. The LCR MSCP (2016), summarizing the literature, states that breeding sites consist of "…ponds, slow-moving streams, temporary pools, or manmade structures that hold water." More fully (LCR MSCP 2016),

> *"The breeding habitat of Colorado River toads includes seasonal and permanent pools (Fouquette 1970; NatureServe 2006; Wright and Wright 1949* in *Fouquette, Jr., et al. 2005) … They are also known to use artificial water bodies, such as canals, flood control impoundments, stock tanks, water irrigation ditches, and reservoirs (Gergus et al. 1999; Musgrave and Cochran 1930; Blair and Pettus 1954; Degenhardt et al. 1996). Blair and Pettus (1954) observed a breeding aggregation in a large stock tank. This species has been found inhabiting flood control sites at Adobe Dam and Cave Buttes and a cattle tank west of the Verde River in north-central Maricopa County, Arizona (Sullivan and Fernandez 1999; Sullivan and Malmos 1994). King and Robbins (1991) describe agricultural drains, dam seepages, irrigation canals, and backwaters along the LCR as marginal habitat for this species.*

Kiesow (2015) and Kiesow and Griffis-Kyle (2017) add tinajas to the list of natural pool types, based on observations in Goldwater Range-East. The literature does not indicate what flow velocities CRTO tolerate in their selection of breeding sites in "slow-moving streams" or in irrigation ditches or canals.

Additionally, as noted above (see this chapter, "Fire Regime"), extreme erosion from a watershed—e.g., following upland fires or following highly erosive downpours—can result in the filling of former pools with sediment along the downstream waterways. Parker (2006) observed this chain of events following upland fires in the Rincon Mountains in Saguaro National Park above Tucson, Arizona, that filled in tinajas and other former pool locations along downstream waterways, leading to local extirpations of the lowland leopard frog. Again, CRTO use of seasonal pools as breeding sites along such waterways presumably would make them vulnerable to such causal chains as well.

Extreme runoff events may affect CRTO in other ways as well. Kiesow (2015) notes that significant flow events from runoff in Goldwater Range-East can scour out the accumulated organic matter from seasonal pools (in this case tinajas) along natural drainage channels but not from artificial catchments along these flow paths. This, in turn, affected the subsequent chemistry of the water in these two types of water bodies, including resulting in a more rapid and higher buildup of ammonia (Griffis-Kyle et al. 2019). High flow events can also affect monitoring. O'Donnell and Leavitt (2017a, 2017b) note that a flood destroyed or displaced DAR equipment for monitoring amphibian mating calls along the Big Sandy River on one occasion.

Chapter 5 – Controlling Factors

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

The seven controlling factors identified in this CEM do not constitute individual variables; rather, each consists of a category of variables (including human activities) that share important features , making it useful to treat these variables together. In particular, each controlling factor covers activities that are (1) shaped by a single body of policies or institutions and (2) have 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 CEMs across the LCR MSCP.

Table 4 lists the seven controlling factors included in the CRTO conceptual ecological model and the habitat elements they are proposed to directly affect. Controlling factors also may affect habitat elements indirectly through their effects on other controlling factors or through the cascading effects of habitat elements on each other.

The authors of this CEM considered including an eighth controlling factor to address the causes of private collecting of CRTO. Chapter 1 (see "Colorado River Toad Life Stage 3 – Adults" and chapter 4 (see "Monitoring, Capture, Handling") discuss the reasons for such private collecting; however, the literature reviewed for this CEM does not provide information on the magnitude, timing, frequency, or spatial distribution of such collecting, let alone information on its effects on local CRTO abundances. The authors therefore decided not to include a controlling factor to address the private collecting of CRTO; the CEM can be updated if sufficient information accumulates to clarify the situation. This CEM does include private collecting as an aspect of the habitat element, "Monitoring, Capture, Handling," without identifying any controlling factor(s) for this activity.

Table 4.—CRTO controlling factors and the habitat elements they are proposed to directly affect among the three life stages

(Xs indicate which controlling factors are proposed to directly affect which habitat elements [**X** = unidirectional; ***X*** = bi-directional].)

Habitat element ➔ / Controlling factor ⬇	Arthropod community	Chemical contaminants	Fire regime	Infectious agents	Monitoring, capture, handling	Periphyton & pom	Temperature	Vegetation assemblage	Vertebrate community	Water availability
Conservation monitoring & research programs					X					
Fire management			***X***							
Habitat development & management		X	X					X	X	
Land use	X	X						X	X	X
Nuisance species introduction & management	X			X		X		X	X	
On-site water management		X								X
Water storage-delivery system design & operation		X								X

CONSERVATION MONITORING & 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 to potentially benefit 5 evaluation species. The HCP identifies CRTO as an evaluation species (LCR MSCP 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 CRTO (LCR MSCP 2018a, 2018b).

Fire Management

Full name: **The types, frequencies, and duration of activities intended to control and/or suppress fire at locations within the greater LCR ecosystem.** The LCR MSCP and other land management agencies along the LCR and Bill Williams River valleys actively manage wildfires through fire suppression, and the construction of fire control breaks, and may use prescribed fire as a management tool (Reclamation 2018). Wildfire is a natural type of disturbance in the riparian plant communities of the Lower Colorado River Valley, and wildfires today also occur through human accidents (Conway et al. 2010; LCR MSCP 2018a; Mac Nally 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).

Habitat Development & Management

Full name: **The types, frequencies, and durations of actions taken by the LCR MCP and its partners to create and manage habitat for species conservation, including actions to affect the taxonomic composition, abundance, condition, and spatial distribution of vegetation**. The HCP (LCR MSCP 2004) directs the LCR MSCP to carry out conservation measures to meet the biological needs of 6 threatened or endangered species and 21 other covered species, and to potentially benefit 4 evaluation species. These measures include creating and managing habitat to meet these biological needs through the manipulation particularly of vegetation and hydrology. The LCR MSCP and other land and water managers along the LCR and Bill Williams River valleys use a range of methods to establish and manage the vegetation on lands under their authorities, including prescribed fire, surface irrigation and subirrigation, planting, fertilizing, thinning and hand removal, disking and plowing, and the application of herbicides (LCR MSCP 2004, 2014, 2018a). Agencies and irrigation and drainage districts may also remove vegetation to maintain roads and canals under their authorities.

As noted in chapter 1, CRTO historically occurred in the United States along and west of the Lower Colorado River Valley into southeastern California but currently in the greater LCR ecosystem only occur only in scattered locations along the east side of the valley in La Paz and Yuma Counties, Arizona, including in the Bill Williams River watershed below Alamo Dam. Nevertheless, this CEM addresses the historic area of distribution of CRTO, not just the portions that lie within the LCR MSCP planning area.

LAND USE

Full name: **The types, frequencies, and duration of major land-use activities taking place on lands that surround locations with existing or potential CRTO breeding or foraging habitat within the greater 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 (LCR MSCP 2004). Major landowners along the LCR and Bill Williams River valleys in Arizona include the Bureau of Land Management; State of Arizona; USFWS; Reclamation; the Chemehuevi, Cocopah, Mohave, and Quechan Indian Tribes; and private individuals.

Airborne chemical 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; Mann et al. 2009; Smalling et al. 2015; Sredl et al. 1997b). Agricultural fields occur in close proximity to potential CRTO habitat sites identified by the AZGFD along the main stem LCR valley (Cotten 2011; Cotten and Grandmaison 2013; Cotten and Leavitt 2014a). Herbicides and pesticides are widely used on alfalfa and cotton, which are both grown extensively in the LCR valley, with aerial application common. Agricultural chemicals—including herbicides, pesticides, and fertilizers—potentially can drift in the air to reach CRTO habitat downwind of intended application 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). As noted in chapter 4 (see "Chemical Contaminants"), no irrigation agriculture is present upstream of or surrounding CRTO habitat in the Bill Williams River watershed. Further, the literature and experts consulted to prepare this CEM do not identify any specific airborne chemical contaminants of potential concern for CRTO habitat sites along the Bill Williams River valley or potential CRTO habitat along the LCR valley.

NUISANCE SPECIES INTRODUCTION & MANAGEMENT

Full name: **The introduction and management of nuisance species that potentially may interact with CRTO or their habitat within the greater LCR ecosystem**. Nuisance species are non-native animals, plants, and micro-organisms, which 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 it includes both intentional and accidental introductions. Management activities may include, but are not limited to, 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; the Chemehuevi, Cocopah, Mohave, and Quechan Indian Tribes; and irrigation districts.

Nuisance species of potential concern for the conservation of CRTO along the LCR and Bill Williams River valleys include saltcedar (see chapter 4, "Vegetation Assemblage"), the American bullfrog and possibly numerous predatory non-native fishes (see chapter 4, "Vertebrate Community"), northern crayfish and red swamp crayfish (see chapter 4, "Arthropod Community"), and *Bd*, the fungus responsible for chytridiomycosis (see chapter 4, "Infectious Agents").

It should also be noted that natural resource managers in the Southwestern United States initially used herbicides as one tool to control saltcedar, along with prescribed fire and mechanical removal. However, the use of herbicides to control saltcedar in the region has become much less frequent over the past decade due to the success of biocontrol efforts using northern tamarisk beetles (see chapter 4, "Arthropod Assemblage").

ON-SITE WATER MANAGEMENT

Full name: **The types, frequencies, and durations of actions taken to manage the delivery and distribution of regulated water to areas with existing or potential CRTO breeding or foraging habitat within the greater 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 in chapter 4 (see "Water Availability"), CRTO can use artificial features such as catchment basins, earthen cattle tanks, and irrigation canals and ditches as breeding sites. The LCR MSCP and USFWS irrigate portions of several conservation areas along the Lower Colorado River Valley to create and manage habitat for general wildlife, LCR MSCP covered species, and associated wetland habitat (LCR MSCP 2018a). In addition, given the flexibility that CRTO exhibit in their selection of breeding habitat, the numerous agricultural irrigation and drainage districts along the Lower Colorado River Valley unintentionally could create additional potential CRTO habitat along their surface waterways. Once established in an area with breeding sites wetted by on-site water management, CRTO likely would continue to occupy the area only so long as those particular water management practices continue.

WATER STORAGE-DELIVERY SYSTEM DESIGN & 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 and releases of water from Alamo Dam on the Bill Williams River**. The Colorado River through the Lower Colorado River Valley consists of a chain of reservoirs separated by flowing reaches. The water moving through this system is highly regulated by Reclamation for storage and delivery to numerous international, Federal, State, Tribal, municipal, and agricultural holders of water rights, as well as for hydropower generation. 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 (LCR MSCP 2004). The dams along and above the LCR also trap essentially all 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 for the use of that water 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.

The U.S. Army Corps of Engineers manages Alamo Dam on the Bill Williams River and its impoundment, Alamo Lake, for purposes of flood control, water

conservation, recreation, and fish and wildlife benefits. Operations of the dam affect the amount, timing, and frequency of availability of surface water along the Bill Williams River floodplain below the dam, an area in which CRTO are known to occur. The waters regulated by Alamo Dam are also considered parts of the waters of the Colorado River Basin for purposes of water management at the basin scale.

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains three sections, each presenting the CEM for a single CRTO 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.

This 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 in order to give the reader an overall sense of the CEM for each life stage.

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

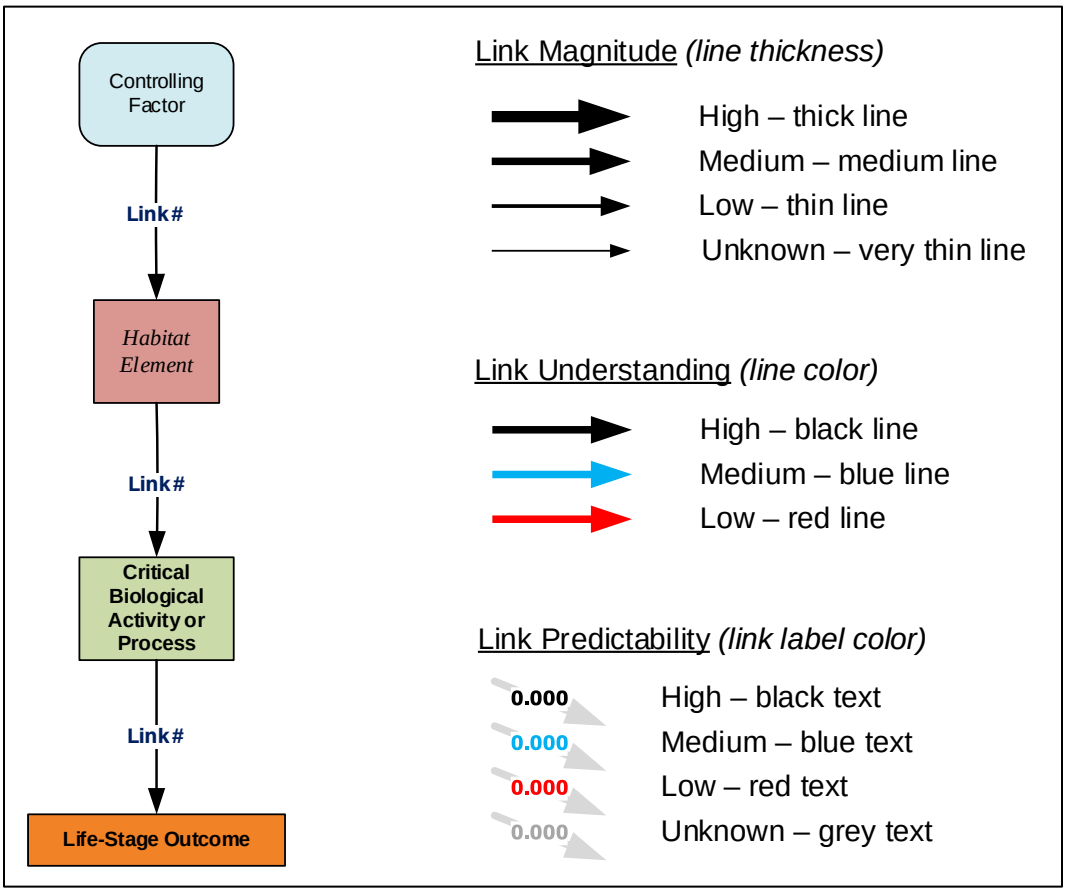

Figure 2.—Diagram conventions for LCR MSCP species conceptual ecological models.

The conventions for displaying information about the causal links are as follows: Links are represented by arrows, the point of which indicates the direction of causation. Bi-directional causal links are represented by arrows with points at both ends. The thickness of the arrow represents link magnitude, 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. 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 are proposed to strongly affect the outcomes for each life stage and identify important causal relationships proposed to have high scientific uncertainty. The latter constitute topics of potential importance for adaptive management investigation. The remainder of this chapter summarizes the CEM for each life stage under four headings: Effects of life-stage outcomes on each other; effects of critical biological activities and processes on life-stage outcomes; effects of critical biological activities and processes on each other; and effects of habitat elements on critical biological activities and processes. The effects of habitat elements on each other, and the effects of controlling factors both on each other and on habitat elements, are discussed in chapter 7.

LIFE STAGE 1 – EGGS

As described in chapter 2, the CRTO eggs life stage begins when adult females deposit their eggs in a shallow, still or very-low-velocity, permanent or seasonal water body during the summer monsoonal season. The life stage ends when the embryos emerge from their natal egg mass as hatchlings, which this CEM addresses as part of the succeeding larvae and metamorphs life stage. Based on limited observations, this life stage appears to span only 1 to 2 days. The CEM recognizes two life-stage outcomes: egg growth, and egg survival. Figure 3 (at the end of this section) presents the complete CEM for this life stage, showing all controlling factors, habitat elements, critical biological activities and processes, life-stage outcomes, and their linkages.

Effects of Life-Stage Outcomes on Each Other

This CEM proposes that CRTO egg growth affects egg survival, but with unknown magnitude. As noted above (see also attachment 1), link magnitude refers to the degree to which a given component of the model controls some

condition relative to other components affecting that same condition. Theoretically, faster maturation in CRTO eggs should convey lower vulnerability to threats specific to the eggs life stage and, therefore, lead to a higher rate of survival. The relationship should be strong, based on core biological principles, even though the life stage is brief. However, no studies have been conducted to address the topic specifically for CRTO or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is rated as low.

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

This CEM identifies five critical biological activities or processes that directly affect one or both outcomes for this life stage: chemical stress, disease, mechanical stress, predation, and thermal stress. As shown on figure 3, all effects of these five critical biological activities and processes on CRTO egg survival and/or growth are rated as poorly understood (low understanding), reflecting a broad lack of published information on the details of the entire life stage. This lack of available information is also reflected in the ratings of "unknown" for link magnitude for most effects of the five critical biological activities and processes on either egg life-stage outcome.

However, this CEM does propose link magnitudes other than "unknown" for the effects of two critical biological activities or processes on egg survival. Specifically, it hypothesizes that chemical stress and thermal stress have low-magnitude direct effects on egg survival. These two ratings reflect the existence of at least some information on which to base a rating. There are no reports of chemical stress among CRTO eggs in the greater LCR ecosystem or elsewhere. However, some potential chemical stressors (e.g., selenium, ammonia) are known to occur in the water in some localities within the ecosystem that CRTO might use as breeding sites. Similarly, there are no reports of thermal stress or its effects in CRTO eggs in the greater LCR ecosystem or elsewhere, but thermal stress is a commonly recognized cause of impaired development in amphibian eggs. This CEM rates link magnitude as low for these two links based on three assumptions: (1) that chemically problematic water bodies are not common in the greater LCR ecosystem, (2) that CRTO will not frequently breed in waters that are thermally unsuitable, and (3) that the eggs life stage is too brief for significant chronic effects to accumulate.

Effects of Critical Biological Activities and Processes on Each Other

This CEM proposes that four critical biological activities or processes for this life stage affect each other, possibly compounding their effects on egg growth or survival. Specifically, it proposes (1) that the rates of both chemical stress and thermal stress affect the rate of disease in CRTO eggs, (2) that the rate of disease reciprocally affects the rates of both chemical stress and thermal stress, and (3 that the rate of predation affects the rate of mechanical stress (non-lethal injury) in CRTO eggs. This CEM rates the magnitude of the effects of chemical stress and disease on each other as low based on general knowledge that these two forms of stress can reinforce each other among amphibians during this developmental stage. Otherwise, it identifies the magnitudes of all links among critical biological activities and processes as unknown, with proposed low understanding, due to the lack of published information on these topics for this or any closely related species. The CEM proposes these links based on suggestions in the published literature on CRTO and on basic principles of toad biology. It includes the link between predation and mechanical stress while recognizing that most injuries to CRTO eggs from predator attacks likely will result directly in mortality rather than any persistent mechanical stress. However, CRTO egg masses are large and linear, and it is conceivable that a predator could merely dislodge and damage some parts of an egg mass while consuming others.

Effects of Habitat Elements on Critical Biological Activities and Processes

This CEM proposes that one habitat element directly affects two critical activities or processes and seven other habitat elements each directly affects one critical biological activities or processes for the CRTO eggs life stage. However, it proposes that all nine of these links are poorly understood (low understanding) and rates seven of these links as having unknown magnitude.

Specifically, this CEM proposes that, logically, chemical contaminants and water temperature in the water bodies where CRTO deposit their eggs affect the rates of, respectively, chemical stress and thermal stress on this life stage, but with low magnitude. These two ratings for link magnitude rest on three assumptions: (1) that chemically problematic water bodies are not common in the greater LCR ecosystem, (2) that CRTO will not frequently breed in waters that are thermally unsuitable, and (3) that the eggs life stage is too brief for significant chronic effects of either type of stress to accumulate.

Otherwise, this CEM proposes the following links but rates them as having unknown magnitude: (1) the spectrum and abundance of infectious agents in these water bodies should affect the rate of disease among CRTO eggs; (2) the fire regime around these water bodies conceivably could affect the incidence of thermal stress; (3) water availability should affect the incidence of chemical stress (the CEM categorizes hydration stress as a form of chemical stress); (4) the make-up of the community of arthropods that live in or visit these water bodies should affect the rate of predation; (5) the make-up of the community of vertebrates that live in or visit these water bodies similarly should affect the rate of predation; (6) water availability in the form of flash floods and other high-velocity flow events through these water bodies could affect the rate of mechanical stress; and (7) monitoring and handling of CRTO eggs by investigators also could affect the rate of mechanical stress. As noted above, this CEM proposes that these seven links are all poorly understood (low understanding) but recognizes their possibility based on basic principles of desert amphibian biology.

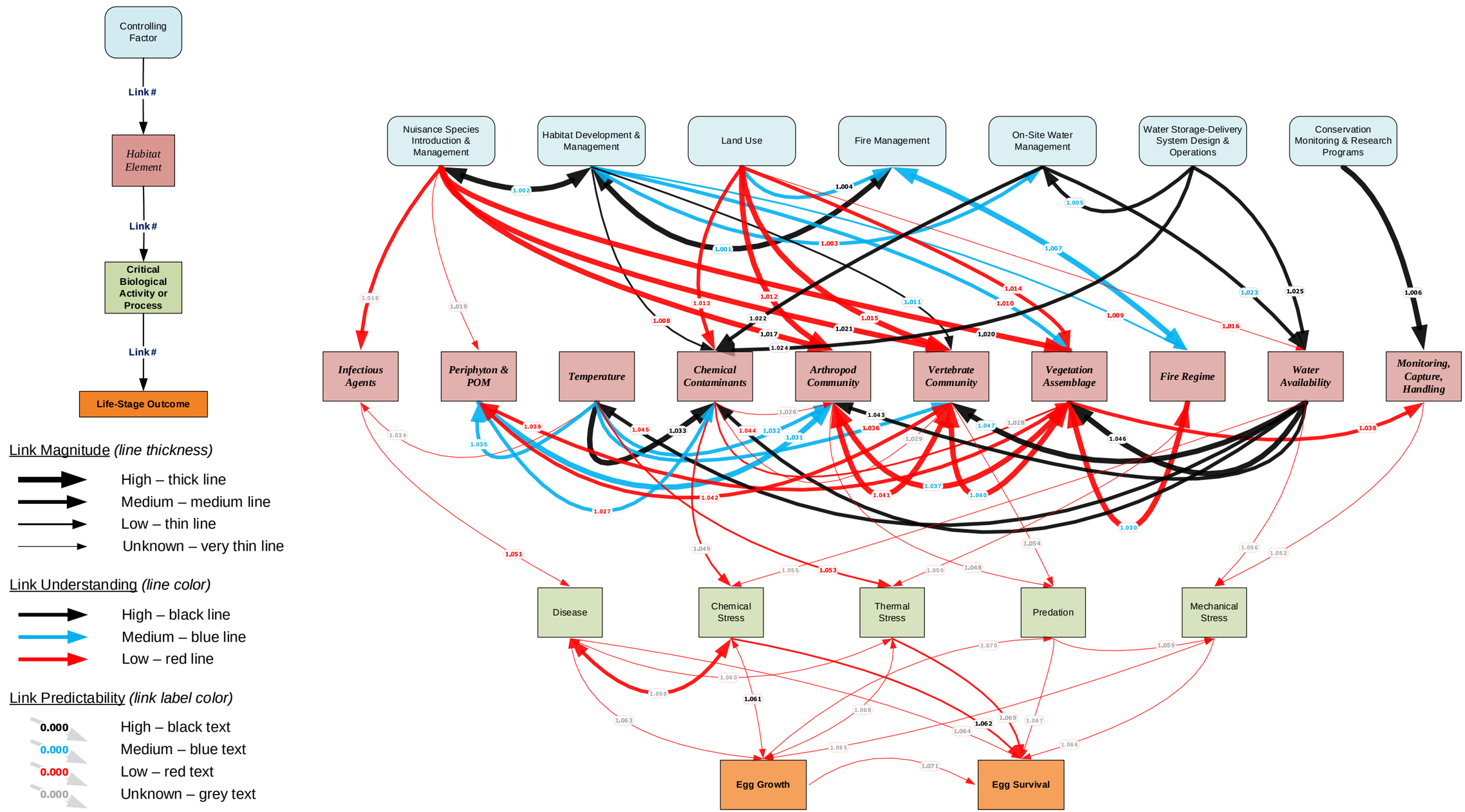

Figure 3.—CEM master diagram for CRTO life stage 1 – eggs life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LIFE STAGE 2 – LARVAE AND METAMORPHS

As described in chapter 2, the CRTO larvae and metamorphs life stage begins when the eggs hatch and the new larvae (hatchlings) swim away from the remains of their natal egg mass as tadpoles with eyes, a tail, and external gills. As with all anurans, the CRTO larvae and metamorphs life stage ends with the completion of metamorphosis. Limited observations indicate that this life stage spans a month or less. This CEM recognizes two life-stage outcomes: larval-metamorph growth, and larval-metamorph survival. Figure 4 (at the end of this section) presents the complete CEM for this life stage, showing all controlling factors, habitat elements, critical biological activities and processes, life-stage outcomes, and their linkages.

Effects of Life-Stage Outcomes on Each Other

Similar to the CEM for the eggs life stage, the CEM for the next life stage proposes that CRTO larval-metamorph growth affects larval-metamorph survival, but with unknown magnitude. Again, as noted above (see also attachment 1), link magnitude refers to the degree to which a given component of the model controls some condition relative to other components affecting that same condition. Theoretically, faster maturation in CRTO larvae and metamorphs should convey lower vulnerability to threats specific to the larvae and metamorphs life stage and, therefore, lead to a higher rate of survival. The relationship should be strong, based on basic biological principles. However, no studies have been conducted to address the topic specifically for CRTO or any closely related species. As a result, the magnitude of this link is unknown, and link understanding is rated as low.

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

This CEM identifies six critical biological activities or processes that directly affect one or both outcomes for this life stage: chemical stress, disease, foraging, mechanical stress, predation, and thermal stress. As shown on figure 4, all effects of these six critical biological activities and processes on CRTO larval-metamorph survival and/or growth are rated as poorly understood (low understanding), reflecting a broad lack of published information on the details of the entire life stage. This lack of available information is also reflected in the ratings of “unknown” for link magnitude for many—but not all—effects of these six critical biological activities and processes on either of the two life-stage outcomes.

This CEM does propose link magnitudes other than "unknown" for the effects of one critical biological activity or process on larval-metamorph growth and the effects of three critical biological activities or processes on larval-metamorph survival. Specifically, it hypothesizes that the success rate for CRTO larval-metamorph foraging has a high-magnitude direct effect on both larval-metamorph growth and larval-metamorph survival and that both chemical stress and thermal stress have low-magnitude direct effects on larval-metamorph survival.

The high-magnitude ratings for the effects of foraging success rest on basic biological principles. Foraging success is necessary for survival and also promotes growth and healthy body condition. Reciprocally, impaired body condition can reduce foraging success. However, the literature reviewed for this CEM provides no information on CRTO larval foraging, such as information on food item selection, and no information on variability in foraging success. As noted in chapter 2, CRTO metamorphs, as with all anuran metamorphs, obtain all their nutrition through resorption of their tails and do not forage.

The low-magnitude ratings for the effects of chemical and thermal stress on CRTO larval-metamorph survival also rest on basic biological principles rather than observations of CRTO. The literature reviewed for this CEM contains no reports of chemical stress among CRTO larvae or metamorphs in the greater LCR ecosystem or elsewhere. However, some potential chemical stressors (e.g., selenium, ammonia) are known to occur in the water in some localities within the ecosystem that CRTO might use as breeding sites. Similarly, the literature reviewed contains no reports of thermal stress or its effects in CRTO larvae or metamorphs in the greater LCR ecosystem or elsewhere. However, thermal stress is a commonly recognized cause of impaired development in amphibian larvae and metamorphs. This CEM rates link magnitude as low for these two links based on three assumptions: (1) that chemically problematic water bodies are not common in the greater LCR ecosystem, (2) that CRTO will not frequently breed in waters that are thermally unsuitable, and (3) that the rapid maturation of CRTO larvae and metamorphs allows them to reach adulthood and escape most temporary natal pools before they become overly warm following their creation by seasonal rainstorms and runoff.

Effects of Critical Biological Activities and Processes on Each Other

This CEM proposes that eight critical biological activities or processes for this life stage—chemical stress, competition, disease, foraging, mechanical stress, predation, resting/hiding, and thermal stress—affect or are affected by other

critical biological activities or process, possibly compounding their effects on CRTO larval-metamorph growth or survival. Specifically, this CEM proposes the following:

- The rate of chemical stress affects the vulnerability of CRTO larvae and metamorphs to disease. Reciprocally, the rate of disease in CRTO larvae and metamorphs affects the vulnerability of the larvae and metamorphs to chemical stress. This CEM rates this bi-directional link as having a medium magnitude and low understanding.

- The rate of competition for food items that CRTO larvae encounter from conspecifics and other species affects the CRTO larval rate of foraging success. This CEM rates this unidirectional link as having a medium magnitude and low understanding.

- The rate of predation on CRTO larvae and metamorphs affects the rate at which the larvae and metamorphs are injured (experience mechanical stress) in failed predator attacks. This CEM rates this unidirectional link as having unknown magnitude and low understanding.

- The effectiveness of CRTO larval and metamorph abilities to move (resting/hiding behaviors) to keep themselves wetted and cool affects the rates at which they experience hydration stress (identified as a form of chemical stress in this CEM) and thermal stress. Reciprocally, chemical (hydration) and thermal stress can impair the ability of CRTO larvae and metamorphs to move to suitable resting/hiding locations within their natal water body. This CEM rates these two bi-directional links as having low magnitude and low understanding.

- The rate of thermal stress affects the vulnerability of CRTO larvae and metamorphs to disease. Reciprocally, the rate of disease in CRTO larvae and metamorphs affects the vulnerability of the larvae and metamorphs to thermal stress. This CEM rates this bi-directional link as having medium magnitude and low understanding.

The ratings of medium and low magnitude among these several links rest on basic biological principles and known relationships in anuran larval and metamorph biology and ecology in general. The ratings of low understanding reflect a lack of published information on these topics for CRTO or any closely related species.

Effects of Habitat Elements on Critical Biological Activities and Processes

This CEM identifies eight habitat elements that may directly affect one or more critical biological activities or processes in the CRTO larvae and metamorphs life stage. Each of these eight habitat elements is proposed to directly affect at least one critical biological activity or process. However, only two habitat elements are proposed to have high-magnitude direct effects on any critical biological activity or process, two are proposed to have medium-magnitude direct effects, and two are proposed to have low-magnitude direct effects. This CEM assigns a rating of unknown to link magnitude for all other direct effects of habitat elements on critical biological activities or processes in this life stage. Specifically, the CEM for the CRTO larvae and metamorphs life stage proposes the following:

- The composition and other characteristics of the arthropod community in and immediately around CRTO breeding sites have a high-magnitude effect on CRTO larval-metamorph foraging, as CRTO larvae consume smaller arthropods and their larvae as parts of their diet. This link is proposed to be moderately well understood.

- The composition and other characteristics of the arthropod community in and immediately around CRTO breeding sites have a high-magnitude effect on the intensity of predation that CRTO larvae and metamorphs face, as aquatic arthropods, including crayfish, and many insect larvae are known predators of amphibian larvae and metamorphs in general. However, the literature reviewed for this CEM provides no direct evidence of predation on CRTO larvae or metamorphs and, therefore, rates the link as poorly understood.

- CRTO larvae are thought be algivorous and omnivorous, based on evidence for similar species worldwide. Thus, theoretically, CRTO larval foraging success should be greater, the greater the diversity and abundance of periphyton and POM. This CEM rates the magnitude of this link as high. However, the subject apparently has not been studied specifically for CRTO, warranting a rating of low for understanding.

- The composition and other characteristics of the vertebrate community in and immediately around CRTO breeding sites have a high-magnitude effect on the intensity of predation that CRTO larvae and metamorphs face. Aquatic and terrestrial vertebrates, including small fishes, carnivorous larvae of other amphibians, predatory wading birds, and snakes are known predators of amphibian larvae and metamorphs in general. However, the literature reviewed for this CEM provides no direct evidence of predation on CRTO larvae or metamorphs and, therefore, rates the link as poorly understood.

- The composition and other characteristics of the arthropod community in CRTO breeding sites have a medium-magnitude effect on the intensity of competition that CRTO larval-metamorphs face for food items. Many aquatic arthropods have diets that may overlap that of CRTO larvae. However, this link is proposed to be poorly understood.

- The composition and other characteristics of the vertebrate community in CRTO breeding sites have a medium-magnitude effect on the intensity of competition that CRTO larval-metamorphs face for food items. Many small aquatic vertebrates, including small fishes and larvae of other amphibians, have diets that may overlap that of CRTO larvae. However, this link is proposed to be poorly understood.

- Theoretically, the types and concentrations of chemical contaminants in the water in CRTO breeding sites should affect the types and intensity of chemical stress that CRTO larvae and metamorphs may experience. This CEM rates link magnitude as low based on an assumption that chemically problematic water is not common in existing or potential CRTO breeding sites in the greater LCR ecosystem. However, this link is proposed to be poorly understood.

- Theoretically, the magnitude and duration of water temperature extremes in CRTO breeding sites should affect the types and intensity of thermal stress that CRTO larvae and metamorphs may experience. This CEM rates link magnitude as low based on assumptions that CRTO will not frequently breed in waters that are thermally unsuitable and that the rapid maturation of CRTO larvae and metamorphs allows them to reach adulthood and escape most temporary natal pools before they become overly warm following their creation by seasonal rainstorms and runoff. However, this link is proposed to be poorly understood.

- Theoretically, the fire regime should affect the risks that CRTO larvae and metamorphs face from thermal stress; the types of infectious agents present should affect the risks that CRTO larvae and metamorphs face from disease; monitoring, capture, and handling practices should affect the risks that CRTO larvae and metamorphs face from mechanical stress and from disruption of their resting/hiding behaviors; the vegetation assemblage in and around breeding sites, and litter from this vegetation, should affect the availability of cover for CRTO larval and metamorph resting/hiding; and water availability should affect the risks that CRTO larvae and metamorphs face from both chemical (hydration) and mechanical stress. However, the literature specifically on CRTO reviewed for this CEM provides no information on any of these potential links. Consequently, this CEM rates their magnitudes as unknown and understanding as low.

Finally, this CEM proposes that CRTO larval-metamorph resting/hiding behaviors reciprocally affect monitoring of this life stage. The ability of CRTO larvae and metamorphs to hide affects the ability of visual monitoring to detect them, and their ability to scatter and hide affects the ability of some capture methods. However, this relationship has not been studied and, consequently, is rated as poorly understood.

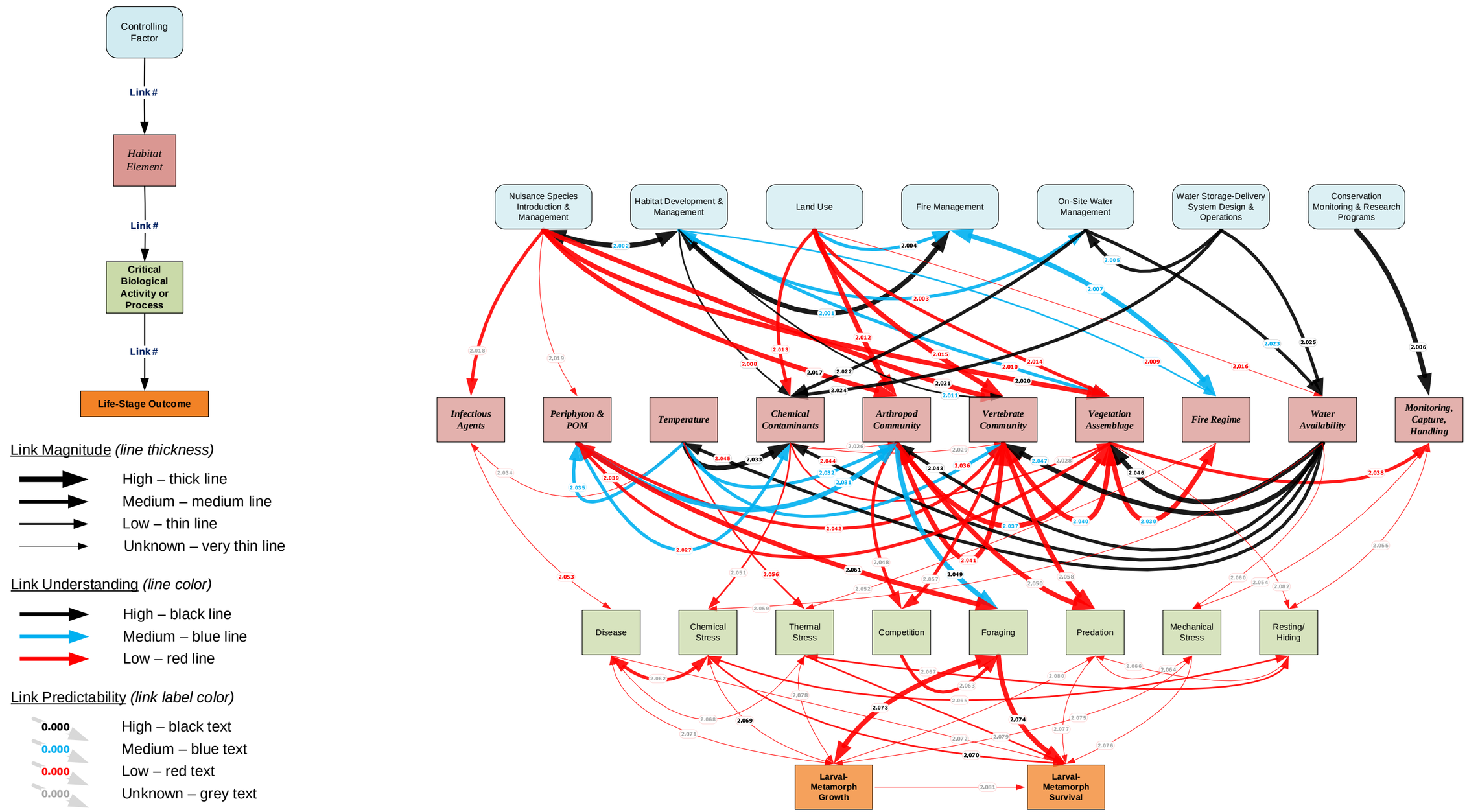

Figure 4.—CEM master diagram for CRTO life stage 2 – larvae and metamorphs life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

LIFE STAGE 3 – ADULTS

As described in chapter 2, the CRTO adults life stage begins with the completion of metamorphosis and lasts through the remainder of the toad's life. Limited evidence indicates that CRTO adults become sexually mature by the time they reach 2 years of age and live for another 2 or 3 years after sexual maturity. The CEM for the CRTO adults life stage has three life-stage outcomes: adult growth, adult survival, and adult fertility. 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.

Effects of Life-Stage Outcomes on Each Other

Similar to the CEMs for the preceding two life stages, the CEM for the adults life stage proposes that CRTO adult growth affects adult survival and *vice versa*, but with unknown magnitude. Again, as noted above (see also attachment 1), link magnitude refers to the degree to which a given component of the model controls some condition relative to other components affecting that same condition. Theoretically, faster growth to full body size in CRTO adults should convey lower vulnerability to threats such as predation and mechanical stress and, therefore, lead to a higher rate of survival. Reciprocally, CRTO continue growing as long as they live, although apparently at a slower rate as they get older. The relationship should be strong in both directions, based on basic biological principles and speculation in species accounts. However, no studies have been conducted to address the topic specifically for CRTO. As a result, the magnitude of this link is unknown, and link understanding is rated as low.

This CEM also proposes that CRTO adult growth and survival both affect adult fertility with high magnitude, based on the following reasoning:

- CRTO adults do not become fertile until they reach sexual maturity. The faster they grow to maturity, the sooner they become fertile. Further, among anurans in general, larger females typically produce larger clutches and sometimes also larger eggs within clutches. Finally, among anurans in general, larger males are more likely to mate than are smaller males. However, concerning this last aspect of the relationship, studies document smaller (but sexually mature) CRTO males using searching behaviors instead of calling behaviors as an alternative strategy to find mates when competing with larger males. These three aspects to the overall relationship are well documented in the general literature on anurans, with limited direct evidence from CRTO specifically on male size and mating behavior. Nevertheless, the overall subject apparently has not been studied in CRTO, warranting an overall rating of low for understanding.

- CRTO adults that do not survive through a given year do not contribute to fertility in that year. This is a basic principle of population biology. However, the relationship apparently has not been studied or documented specifically in CRTO, warranting an overall rating of low for understanding.

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

This CEM identifies seven critical biological activities or processes that directly affect adult growth, survival, or fertility: breeding, chemical stress, disease, foraging, mechanical stress, predation, and thermal stress. Specifically, it proposes the following:

- Breeding success necessarily affects adult fertility, with high magnitude. However, the relationship apparently has not been studied specifically in CRTO, warranting a rating of low for understanding.

- Foraging success necessarily affects adult growth and fertility, with high magnitude. Reciprocally, adult growth presumably affects foraging success, as larger CRTO adults presumably are able to overwhelm a larger range of prey. However, the relationship apparently has not been studied specifically in CRTO, warranting a rating of low for understanding.

- Chemical stress could affect adult fertility, with medium magnitude. The literature reviewed for this CEM indicates that some forms of chemical stress (such as the effects of selenium or pesticide bioaccumulation) can alter reproductive fitness in anurans. However, the spatial and temporal distributions of conditions in which this might occur in CRTO in the greater LCR ecosystem are not documented, and no studies have been conducted to examine this topic specifically in CRTO, warranting a rating of low for understanding.

- Chemical stress could affect adult survival, with low magnitude. Chronic chemical stress is a commonly recognized cause of death in amphibians in general. There are no reports of chemical stress among CRTO in the greater LCR ecosystem, but some potential chemical stressors (e.g., selenium, ammonia) are known to occur in some localities within the ecosystem. CRTO presumably have multiple ways to avoid hydration stress, having evolved in the desert. However, these relationships apparently has not been studied specifically in CRTO, warranting a rating of low for understanding.

- Predation should affect adult survival, but this CEM estimates the magnitude of this effect as low. Predation is a common cause of premature mortality among amphibian adults. However, CRTO adults have a robust suite of mechanisms for discouraging predation (toxic secretions, defensive posturing) and grow large enough to discourage predation from many smaller predators. Camera trap records from the Northern Jaguar Reserve in Mexico demonstrate that even large predators (pumas [*Puma concolor*], coyotes) may avoid them entirely, and only a few species are known or hypothesized to prey on them. This reduces the likelihood that predation is a dominant cause of mortality in CRTO adults. Nevertheless, the topic has not been studied systematically in CRTO, warranting a rating of low for understanding.

- Thermal stress could affect adult growth, and *vice versa*, and it also affects adult survival, all with low magnitude. Chronic thermal stress is a commonly recognized cause of both mortality and impaired body condition and growth in amphibians. However, CRTO in the greater LCR ecosystem likely face few or no situations in which they experience chronic thermal stress, and CRTO adults have capabilities to take refuge from thermally stressful local conditions. Nevertheless, the topics apparently have not been studied in CRTO, warranting a rating of low for understanding.

- Chemical stress could affect adult growth and *vice versa*; disease could affect adult growth, survival, and fertility; and mechanical stress also could affect adult growth, survival, and fertility. Such relationships would be expected based on basic principles of biology and ecology. However, the literature reviewed for this CEM provides no information on which to base any estimate of link magnitude. Consequently, it rates these seven links as having unknown magnitudes and low understanding.

Effects of Critical Biological Activities and Processes on Each Other

This CEM proposes that all 1 critical biological activities or processes for this life stage affect or are affected by other critical biological activities or processes, possibly compounding their effects on the adults life-stage outcomes. Specifically, it proposes the following:

- CRTO adults resting in burrows throughout the day and night during the cooler months and during the warmer daytime hours during the warmer months reduces their risks of thermal stress. The literature reviewed for this CEM considers this causal relationship highly likely and crucial to CRTO persistence throughout their range. This CEM rates both link magnitude and link understanding as high.

- Studies of anuran sensitivity to pollutants note that exposure can increase their sensitivity to disease and *vice versa*. However, this topic has not been studied specifically for CRTO. This CEM rates link magnitude as medium and link understanding as low.

- Theoretically, the abundance and range of species competing with CRTO adults for food (competition) could constrain CRTO adult prey selection and foraging success. Competitors with CRTO adults for food are abundant and ubiquitous in the greater LCR ecosystem. However, many of these competitors are native species among which CRTO have evolved and, therefore, likely have adaptations to reduce the magnitude of the effect. On the other hand, some non-native competitors with CRTO adults for food and/or habitat may pose bigger challenges. The subject has not been studied for CRTO. This CEM rates link magnitude as medium and link understanding as low.

- CRTO also rest in burrows during dry seasons and throughout dry years, a behavior that reduces their vulnerability to hydration stress, which this CEM classifies as a type of chemical stress. Reciprocally, dry summer weather when summer rains fail to materialize in their locality cause CRTO adults to remain in their burrows. CRTO resting/hiding behavior thus both affects and is affected by risks of chemical stress. However, the CEM rates both link magnitude and link understanding as low.

- Hypothetically, CRTO breeding aggregations potentially could attract predators, increasing the potential for predation. Reciprocally, predation on CRTO breeding aggregations could disrupt breeding activity. However, the literature reviewed for this CEM does not address the topic. This CEM rates this bi-directional link as having unknown magnitude and low understanding.

- Hypothetically, CRTO faced with competition for food or burrow habitat might leave the general area of their natal pool to find new habitat. However, the subject apparently has not been studied. This CEM rates this proposed link as having unknown magnitude and low understanding.

- Similarly, hypothetically, the abundance and range of species competing with CRTO adults for burrow habitat could constrain CRTO adult success in finding suitable resting/hiding habitat. Competitors with CRTO adults for burrows are abundant and ubiquitous in the greater LCR ecosystem. However, many of these competitors are native species among which CRTO have evolved and, therefore, likely have adaptations to reduce the magnitude of the effect. On the other hand, some non-native competitors for burrow habitat may pose bigger challenges. However, the subject has not been studied for CRTO. This CEM rates this proposed link as having unknown magnitude and low understanding.

- Hypothetically, a lack of sufficient food items in its non-breeding habitat could stimulate CRTO to disperse in search of better foraging habitat. However, the subject has not been studied, and the CRTO's ability to eat anything they can catch gives them a flexibility to survive in a wide range of conditions of food availability. However, the subject has not been studied. This CEM consequently rates this proposed link as having unknown magnitude and low understanding.

- CRTO adults in their non-breeding habitat appear to obtain most or all of their water from their foods. Foraging success therefore affects their vulnerability to hydration stress, which this CEM classifies as a type of chemical stress. However, the subject apparently has not been studied. The CEM consequently rates this proposed link as having unknown magnitude and low understanding.

- Hypothetically, unsuccessful attacks by predators could wound but not kill CRTO adults, resulting in mechanical stress but not mortality. CRTO toxic secretions and defensive behaviors when approached may deter most predation, as may their size when they reach their full adult mass. However, some vertebrate predators have developed methods for trying to prey on CRTO, and these methods may be more effective on smaller CRTO, such as those recently metamorphosed. In any case, the subject apparently has not been studied. The CEM consequently rates this proposed link as having unknown magnitude and low understanding.

- Hypothetically, CRTO may disperse in search of a suitable burrowing habitat because their initial geomorphic setting provides insufficient options, not simply because they encounter other animals already using available burrows (see discussion above, this chapter, concerning possible effects of competition on aggregation/ dispersion). However, the subject has not been studied. The CEM consequently rates this proposed link as having unknown magnitude and low understanding.

- CRTO may be vulnerable to predation in their resting/hiding habitat (burrows) by burrowing foragers such as badgers and snakes. Burrows in soft soils (e.g., sand) may be particularly vulnerable to predators that dig for their prey, such as badgers. However, the subject apparently has not been studied. The CEM consequently rates this proposed link as having unknown magnitude and low understanding.

- Theoretically, thermal stress increases physiological vulnerability to disease and *vice versa*. However, the subject apparently has not been studied in CRTO or any related species. The CEM consequently rates this proposed link as having unknown magnitude and low understanding.

Effects of Habitat Elements on Critical Biological Activities and Processes

This CEM identifies nine habitat elements that may affect 1 or more critical biological activities or processes in the adults life stage. Each of these eleven habitat elements is proposed to directly affect at least one critical biological activity or process. However, only five habitat elements are proposed to have high-magnitude effects on any critical biological activity or process. Specifically, the CEM for the CRTO adults life stage proposes the following:

- The composition and other characteristics of the arthropod community in CRTO non-breeding habitat have a high-magnitude effect on CRTO adult foraging, as CRTO adults may consume any arthropods they can capture. This link is proposed to be moderately well understood.

- Air temperature appears to play a key role in triggering CRTO breeding, which only takes place at nights with temperatures within a consistent range. The link is proposed to have high magnitude and to be moderately well understood.

- CRTO adults appear to select for specific characteristics in the vegetation community within which they forage (non-breeding habitat), particularly a very low density of shrub and woody vegetation and a low density of canopy cover in general. CRTO also appear to select breeding sites overall and specific locations within these sites that have very low aquatic vegetation densities and no overhanging canopy. Both of these links (vegetation assemblage effects on aggregation/dispersion and on breeding) are proposed to have high magnitudes and to be moderately well understood.

- The composition and other characteristics of the vertebrate community in CRTO non-breeding habitat have a high-magnitude effect on CRTO adult foraging, as CRTO adults may consume any small vertebrates they can capture. This link is proposed to be moderately well understood.

- The composition and other characteristics of the vertebrate community in CRTO breeding and non-breeding habitat have a high-magnitude effect on the intensity of predation on CRTO adults. Predators of CRTO adults appear to be limited to vertebrates that have learned how to avoid contact with or have evolved abilities to tolerate, CRTO toxic secretions. However, these relationships have not been studied and, consequently, this link is proposed to be poorly understood.

- Water availability in three forms—rainfall in the vicinity, the presence of surface water in which to breed, and the nighttime relative humidity at the potential breeding site—is crucial for triggering CRTO breeding. The link is proposed to have high magnitude and to be moderately well understood.

- The compositions and other characteristics of both the arthropod and vertebrate communities in CRTO non-breeding habitat affect the competition that CRTO adults face for food items, with medium-magnitude effects. Some arthropods and vertebrates prey on the same other arthropods and vertebrates on which CRTO also prey. However, these links are proposed to be poorly understood.

- Theoretically, the types and concentrations of chemical contaminants to which CRTO adults are exposed, resulting in chemical stress, should affect CRTO breeding success. This CEM rates link magnitude as low based on an assumption that such exposure is not common in existing or potential CRTO habitat in the greater LCR ecosystem. However, this link is proposed to be poorly understood.

- Theoretically, the types and concentrations of chemical contaminants to which CRTO adults are exposed should affect the types and intensity of chemical stress that CRTO adults may experience. This CEM rates link magnitude as low based on an assumption that chemical contamination is not common in existing or potential CRTO non-breeding and breeding habitat in the greater LCR ecosystem. However, this link is proposed to be poorly understood.

- Theoretically, the magnitude and duration of air temperature extremes in CRTO non-breeding habitat sites should affect the frequency and intensity of thermal stress that CRTO adults may experience. This CEM rates link magnitude as low based on assumptions that CRTO are well adapted to the temperature range of their native geographic range and can cope with temperature extremes, including by entering or remaining in their burrows as needed. However, this link is proposed to be poorly understood.

- Theoretically, VES monitoring activity could cause CRTO adults to seek cover (i.e., could trigger hiding activity). Reciprocally, CRTO adult resting/hiding activity may reduce CRTO adult visibility during VESs. However, the literature reviewed for this CEM does document any systematic surveys of CRTO non-breeding habitat or CRTO adult avoidance behaviors during encounters with investigators either across non-breeding habitat or at breeding habitat. Consequently, this bi-directional link is rated as having unknown magnitude and low understanding.

- This CEM also proposes several possible effects of habitat elements on critical biological activities or processes in the adults life stage, which are suggested by basic principles of anuran biology and ecology, but for which no specific evidence for CRTO. These links with unknown magnitude and low understanding address possible effects of: (1) the arthropod community on the intensity of predation on CRTO adults (do any arthropods prey on CRTO adults?), (2) the fire regime on thermal stress, (3) infectious agents on disease, and (4) and water availability on aggregation/dispersion behavior (aggregation to or dispersion from non-breeding habitat based on water availability) and mechanical stress from flash flood events.

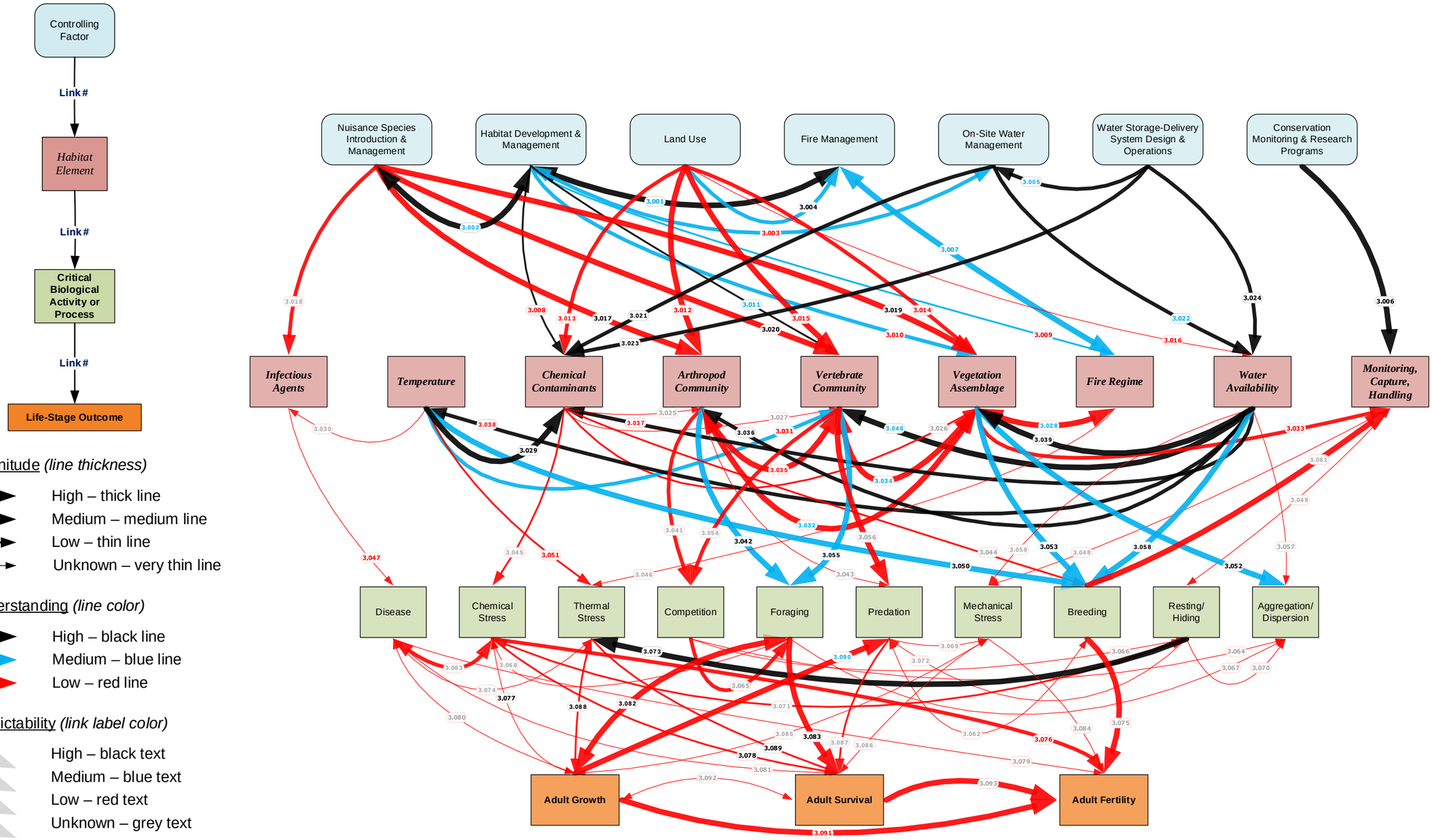

Figure 5.—CEM master diagram for CRTO life stage 3 – adults life stage controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes.

Chapter 7 – Causal Relationships Across Life Stages

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

CAUSAL RELATIONSHIPS AMONG HABITAT ELEMENTS

Chapter 6 documents that each of the 10 habitat elements in the CRTO conceptual ecological model directly affects at least 1 critical biological activity or process in at least 1 life stage (see table 3 in chapter 4). This CEM rates these effects as having high, medium, low, or unknown magnitudes depending on the life stage. However, this CEM proposes that six habitat elements have consistently high- or medium-magnitude effects on critical biological activities and processes across all three life stages: the arthropod community, periphyton & POM, temperature, the vegetation assemblage, the vertebrate community, and water availability. In turn, five of these six dominant habitat elements are affected with high or medium magnitude by one or more other habitat elements, including each other. Specifically, this CEM proposes the following:

- The fire regime affects the vegetation assemblage and *vice versa*, with high magnitude. However, the specific dynamics of fire and its effects on vegetation across CRTO habitat have not been studied, resulting in a rating of low for understanding.

- The periphyton and POM in CRTO breeding waters affects the arthropod community in these waters with high magnitude. The CEM rates this link as moderately well understood.

- The vegetation assemblage in and around CRTO breeding sites and across CRTO non-breeding habitat affects both the arthropod and vertebrate communities in these settings and *vice versa*, with high magnitude. However, the specific dynamics of these interactions have not been studied, resulting in a rating of low for understanding.

- The vertebrate community in and around CRTO breeding sites and across CRTO non-breeding habitat affects the arthropod community in these settings and *vice versa*, with high magnitude. However, the specific dynamics of these interactions have not been studied, resulting in a rating of low for understanding.

- Water availability in and around CRTO breeding sites and across CRTO non-breeding habitat affects both the vegetation assemblages and vertebrate communities in these settings, with high magnitude. These kinds of dynamics are well understood in southwestern desert settings.

- Water chemistry (chemical contaminants) affects the periphyton in CRTO breeding waters and *vice versa*, with medium magnitude. The CEM rates this link as moderately well understood.

- Air and water temperatures in and around CRTO breeding sites and across CRTO non-breeding habitat affect the arthropod, periphyton, and vertebrate communities in these settings, with medium magnitude. The CEM rates these three links as moderately well understood.

- The vegetation assemblage in and immediately around CRTO breeding sites affects the periphyton and POM in this habitat, with medium magnitude. The CEM rates this link as moderately well understood.

- The vertebrate community in and immediately around CRTO breeding sites affects the periphyton and POM in this habitat and *vice versa*, with medium magnitude. One or more life stages of many of the fish and amphibian species and perhaps one or two reptile species (turtles) in the greater LCR ecosystem consume periphyton and POM, thereby affecting the abundance and composition of the periphyton and POM at individual sites. In turn, the abundance and composition of the periphyton and POM at individual sites shape the abundance and distribution of the fish, amphibian, and reptile life stages that feed on them. However, the specific dynamics of these interactions have not been studied, resulting in a rating of low for understanding.

- Water availability in and around CRTO breeding sites and across CRTO non-breeding habitat affects the arthropod communities in these settings, with medium magnitude. These kinds of dynamics are well understood in southwestern desert settings.

- Water availability can affect water temperature in CRTO breeding sites, as temperatures at permanent water bodies are controlled by the source of the water (surface or groundwater inflow) rather than by air temperature, while the opposite is true of temporary water bodies. These kinds of dynamics are well understood in southwestern desert settings.

Causal Relationships Between Controlling Factors and Habitat Elements

The CRTO conceptual ecological model proposes that each of the seven controlling factors has direct high- or medium-magnitude effects on at least one habitat element. Specifically, the CEM proposes the following:

- Conservation monitoring and research programs have direct high-magnitude effects on monitoring, capture, and handling for all three life stages. The CEM notes that these kinds of interactions are well documented and well understood within the LCR MSCP.

- Fire management practices directly affect the fire regime and *vice versa*, with high magnitude. The CEM notes that these kinds of interactions are moderately well documented and moderately well understood in the greater LCR ecosystem.

- Land use practices around CRTO breeding sites and CRTO non-breeding habitat directly affect the arthropod and vertebrate communities in these habitat settings, with high magnitude. However, these interactions have not been studied specifically as they pertain to CRTO habitat in the greater LCR ecosystem, resulting in CEM ratings of low for understanding.

- Nuisance species introductions and management directly affects the arthropod and vertebrate communities and vegetation assemblages in CRTO breeding and non-breeding habitat throughout the greater LCR ecosystem, with high magnitude. However, while well understood in principle, these interactions have not been studied specifically as they pertain to CRTO habitat, resulting in a CEM rating of low for understanding.

- Habitat development and management efforts can directly affect the vegetation assemblages in CRTO breeding and non-breeding habitat. However, such efforts do not affect all existing or potential CRTO habitat areas in the LCR MSCP planning area, let alone in the greater LCR ecosystem in general, resulting in a rating of medium for link magnitude. The CEM notes that these kinds of interactions are moderately well documented and moderately well understood in the greater LCR ecosystem.

- Land use practices around CRTO breeding sites and CRTO non-breeding habitat directly affect the incidence of chemical contaminants and the condition of the vegetation assemblages in these habitat settings, with medium magnitude. However, these interactions have not been studied specifically as they pertain to CRTO habitat in the greater LCR ecosystem, resulting in CEM ratings of low for understanding.

- Nuisance species introductions and management likely directly affects the incidence of infectious agents relevant to CRTO throughout the greater LCR ecosystem, with medium magnitude. However, these interactions have not been studied, resulting in a CEM rating of low for understanding.

- Both on-site water management and larger-scale water storage-delivery system design and operations directly affect both water availability at CRTO breeding sites, and inputs of potential chemical contaminants into these waters, with medium magnitude. The CEM notes that these kinds of interactions are well documented and well understood within the greater LCR ecosystem.

CAUSAL RELATIONSHIPS AMONG CONTROLLING FACTORS

The CEM identifies several direct effects of controlling factors on each other. These effects, in turn, have cascading effects on habitat elements. Specifically, the CEM proposes the following:

- Habitat development and management efforts in the greater LCR ecosystem directly affect both fire management and nuisance species introductions and management and *vice versa*, with high magnitude. The CEM notes that these kinds of interactions are well documented and well understood within the greater LCR ecosystem.

- Habitat development and management efforts in the greater LCR ecosystem directly affect on-site water management at locations with existing and potential CRTO breeding sites and *vice versa*. However, these effects are limited to habitat conservation areas, which do not encompass all existing and potential CRTO breeding habitat in the greater LCR ecosystem, resulting in a rating of medium for magnitude. The CEM notes that these kinds of interactions are moderately well understood.

- Land use practices around CRTO breeding sites and CRTO non-breeding habitat directly affect fire management decisions that include these habitat settings. The CEM notes that these kinds of interactions are moderately well understood.

- Water storage-delivery system design and operations directly affect on-site water management at many locations with existing and potential CRTO breeding sites. On the other hand, on-site water management may take place independently at other such locations (e.g., through the use of groundwater wells). The CEM therefore rates this relationship as having medium magnitude but notes that these kinds of interactions are well documented and well understood.

Chapter 8 – Discussion and Conclusions

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

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

Table 5.—Proposed magnitudes of causal relationships in the CEM for CRTO in the LCR ecosystem

Cause and effect node types		Proposed link magnitude				Row total
Causal node type	**Effect node type**	**High**	**Medium**	**Low**	**Unknown**	
Controlling factor	Controlling factor	6	9	0	0	**15**
Controlling factor	Habitat element	21	24	9	5	**59**
Habitat element	Habitat element	23	25	3	9	**60**
Habitat element	Activity or process	11	4	7	21	**43**
Activity or process	Habitat element	1	0	0	0	**1**
Activity or process	Activity or process	1	5	3	14	**23**
Activity or process	Life-stage outcome	5	1	8	21	**35**
Life-stage outcome	Activity or process	1	0	0	2	**3**
Life-stage outcome	Life-stage outcome	2	0	0	3	**5**
	Column total	**71**	**68**	**30**	**75**	**244**

Table 6.—Proposed levels of understanding of causal relationships in the CEM for CRTO in the LCR ecosystem

Cause and effect node types		Proposed link understanding			Row total
Causal node type	**Effect node type**	**High**	**Medium**	**Low**	
Controlling factor	Controlling factor	9	6	0	**15**
Controlling factor	Habitat element	21	9	29	**59**
Habitat element	Habitat element	18	11	31	**60**
Habitat element	Activity or process	0	7	36	**43**
Activity or process	Habitat element	0	0	1	**1**
Activity or process	Activity or process	1	0	22	**23**
Activity or process	Life-stage outcome	0	0	35	**35**
Life-stage outcome	Activity or process	0	0	3	**3**
Life-stage outcome	Life-stage outcome	0	0	5	**5**
	Column total	**49**	**33**	**162**	**244**

Table 5 shows that 31% (75 of 244) of all proposed causal links in this CEM, across all life stages combined, were rated as having unknown magnitude. This CEM proposes links with unknown magnitude based on basic principles of toad or anuran biology, and expectations articulated in the literature, but for which no data or anecdotes are yet available for CRTO anywhere, let alone specifically in the greater LCR ecosystem. Further, causal links rated as having unknown magnitude comprise a much greater proportion of the links involving effects of critical biological activities or processes (35 of 59), or effects of life-stage outcomes (5 of 8), than of the links involving effects of habitat elements (30 of 103) or controlling factors (5 of 74). This pattern reflects a lack of either anecdotes or formally collected evidence on several aspects of CRTO biology and behavior that could help inform species or habitat management.

Table 6, in turn, shows that more than 66% (162 of 244) of all proposed links in this CEM, across all life stages combined, were rated as having low understanding. Of those 162 links with low understanding, 75 (46%) were rated as unknown for magnitude, 21 (13%) were rated as having low magnitude, 26 (16%) were rated as having medium magnitude, and 40 (25%) were rated as having high magnitude. The data in table 6 thus more strongly indicates a lack of either anecdotes or formally collected evidence on many aspects of CRTO ecology or biology, or behavior that could help inform species or habitat management.

Second, an assessment of causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes identifies several high-magnitude causal relationships (with differing levels of link understanding). These are not necessarily the only causal relationships that actually strongly affect habitat elements, critical biological activities or processes, or life-stage outcomes. However, the relationships identified in this CEM as high-magnitude links are ones for which the literature reviewed for this CEM provides sufficient information to permit a rating of link magnitude. At least some of the links presently assigned a rating of unknown for magnitude may eventually prove to be high-magnitude relationships as knowledge expands. For the present, the CRTO conceptual ecological model identifies the following as high-magnitude causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes:

- This CEM proposes that four controlling factors have direct, high-magnitude effects on one or more habitat elements. These four are, in alphabetical order: (1) conservation monitoring & research programs, with effects on monitoring, capture, handling; (2) fire management, with effects on the fire regime; (3) land use, with effects on the arthropod and vertebrate communities; and (4) nuisance species introduction & management, with effects on the arthropod community, vegetation assemblage, and vertebrate community. This CEM assigns ratings of low

understanding to four of these relationships, each affecting all three life stages. Chapters 4 and 5 discuss the sources of uncertainty for these causal relationships between controlling factors and habitat elements.

- This CEM proposes that six habitat elements have direct, high-magnitude effects on one or more critical biological activities or processes in one or more life stages. These are, in alphabetical order: (1) the arthropod community, with effects on foraging by CRTO larvae and adults and on predation on CRTO larvae and metamorphs; (2) periphyton & POM, with effects on foraging by CRTO larvae; (3) temperature, with effects on breeding in CRTO adults; (4) the vegetation assemblage, with effects on aggregation/dispersion and breeding in CRTO adults; (5) the vertebrate community, with effects on foraging by CRTO adults and predation on CRTO larvae, metamorphs, and adults; and (6) water availability, with effects on CRTO adult breeding. This CEM assigns ratings of low understanding to three of these relationships, each affecting all or either one or two life stages. Chapters 3 and 4 discuss the sources of uncertainty for these causal relationships between habitat elements and critical biological activities and processes.

- This CEM proposes that one critical biological activity or process, CRTO adult breeding, conversely affects one habitat element, monitoring, capture, handling, and does so with high magnitude. CRTO may not call during breeding, and even when they do, their calls are quiet. These aspects of CRTO behavior limit the effectiveness of VES C/R and DAR methods for detecting breeding CRTO.

- This CEM proposes that seven 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 high-magnitude relationships between habitat elements are: (1) effects of the fire regime on the vegetation assemblage and *vice versa*, (2) effects of periphyton and POM on the arthropod community, (3) effects of temperature on the chemical contamination, (4) effects of the vegetation assemblage on the arthropod and vertebrate communities and *vice versa*, (5) effects of the vertebrate community on the arthropod community and *vice versa*, specifically in CRTO breeding habitat, and (6) effects of water availability on the vegetation assemblage and vertebrate community. This CEM assigns ratings of low understanding to all of the high-magnitude reciprocal cause-effect relationships between habitat elements. Chapter 4 discusses the sources of uncertainty for these causal relationships.

- This CEM proposes that two critical biological activities or processes have direct, high-magnitude effects on one or more life-stage outcomes across the three CRTO life stages. First, breeding in the CRTO adults life stage affects adult fertility, and it also affects adult survival. The latter effect is bi-directional and arises because the adults may be particularly vulnerable to predation while breeding, and predator attacks during CRTO breeding will disrupt the mating process. Second, CRTO adult and larval foraging both affect growth during these life stages, and reciprocally, greater growth during these life stages increases foraging success. This CEM assigns ratings of low understanding to all high-magnitude effects of critical biological activities or processes on CRTO life-stage outcomes. Chapter 3 discusses the sources of uncertainty for these causal relationships.

- This CEM proposes that one critical biological activity or process has direct, high-magnitude effects on one other critical biological activity or process for one life stage. Specifically, CRTO adult resting/hiding behavior affects their vulnerability to thermal stress. This CEM assigns a rating of high to understanding of this relationship. Chapter 3 discusses this link further.

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. In addition, as noted above, understanding may improve for links currently assigned ratings of unknown for magnitude.

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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.*

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

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

(1) The effect of one controlling factor on another

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

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

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

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

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

Each controlling factor may affect the abundance, spatial and temporal distributions, and other qualities of more than one habitat element, and several controlling factors may affect the abundance, spatial or temporal distributions, or other qualities of each habitat element. Similarly, the abundance, spatial and temporal distributions, and other qualities of each habitat element may affect more than one biological activity or process, and the abundances, spatial or temporal distributions, or other qualities of several habitat elements may affect

each biological activity or process. Finally, the rate of each critical biological activity or process may contribute to the rates of more than one life-stage outcome.

Integrating this information across all life stages for a species provides a detailed picture of: (1) what is known, with what certainty, and the sources of this information, (2) critical areas of uncertain or conflicting science that demand resolution to better inform 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, this 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 lower Colorado River 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 (*Note*: tables and figures are found 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 (end of this attachment). The diagram conventions mostly follow those in the ERP methodology (DiGennaro et al. 2012).

The spreadsheet for each CEM contains a separate worksheet for each life stage. Each row in the worksheet for a life stage represents a single causal link. Table 1-7 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 conceptual ecological model, 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.

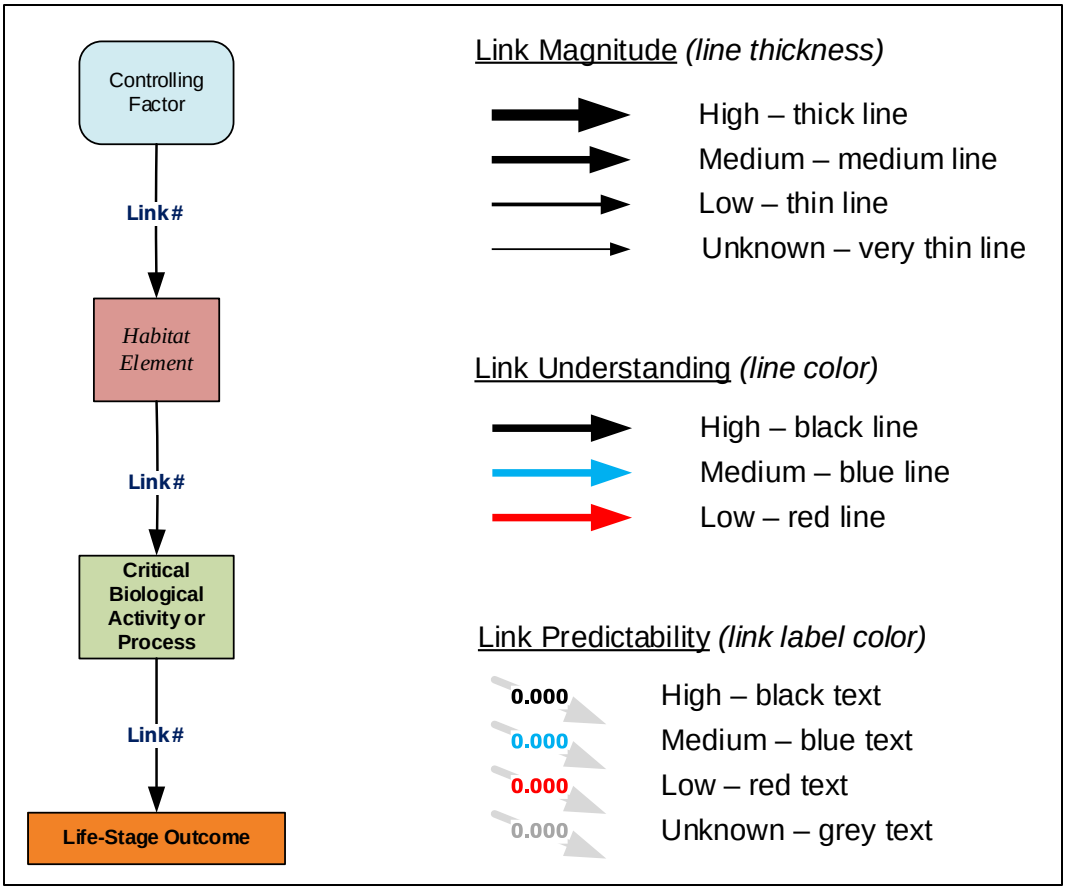

Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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