



Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI) Basic Conceptual Ecological Model for the Lower Colorado River



Photo courtesy of the Bureau of Reclamation



December 2015

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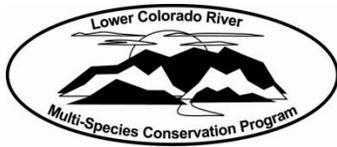
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Lower Colorado River Multi-Species Conservation Program

Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI) Basic Conceptual Ecological Model for the Lower Colorado River

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ACRONYMS AND ABBREVIATIONS

CEM	conceptual ecological model
BEVI	Arizona Bell's Vireo (<i>Vireo bellii arizonae</i>)
Bill Williams River NWR	Bill Williams River National Wildlife Refuge
GBBO	Great Basin Bird Observatory
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
ORV	off-road vehicle(s)
Reclamation	Bureau of Reclamation
USFWS	U.S. Fish and Wildlife Service

Symbols

\geq	greater than or equal to
$<$	less than
%	percent

Definitions

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

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

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

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

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

CONTENTS

	Page
Foreword	v
Executive Summary	ES-1
Conceptual Ecological Models	ES-1
Conceptual Ecological Model Structure	ES-2
Results.....	ES-4
Chapter 1 – Introduction	1
Arizona Bell’s Vireo Reproductive Ecology	1
Conceptual Ecological Model Purposes	2
Conceptual Ecological Model Structure for the BEVI	3
Chapter 2 – BEVI Life Stage Model	7
Introduction to the BEVI Life Cycle	7
BEVI Life Stage 1 – Nest	7
BEVI Life Stage 2 – Juvenile	8
BEVI Life Stage 3 – Breeding Adult.....	8
Life Stage Model Summary	9
Chapter 3 – Critical Biological Activities and Processes	11
Disease	12
Eating	12
Foraging	12
Molt.....	13
Nest Attendance	13
Nest Predation and Brood Parasitism	13
Nest Site Selection	14
Predation	14
Temperature Regulation.....	15
Chapter 4 – Habitat Elements	17
Anthropogenic Disturbance	18
Brood Size.....	19
Canopy Closure.....	19
Community Type	20
Diversity of Vegetation.....	20
Food Availability	21
Genetic Diversity and Infectious Agents	21
Intermediate Structure.....	22
Local Hydrology	22
Matrix Community.....	23
Nest Predator and Cowbird Density	24

	Page
Patch Size.....	24
Parental Feeding Behavior.....	25
Parental Nest Attendance.....	25
Predator Density.....	25
Previous Year’s Use.....	26
Stem Density.....	26
Temperature.....	26
Chapter 5 – Controlling Factors.....	27
Fire Management.....	28
Grazing.....	28
Mechanical Thinning.....	29
Natural Thinning.....	29
Pesticide/Herbicide Application.....	30
Planting Regime.....	30
Recreational Activities.....	30
Water Storage-Delivery System Design and Operation.....	31
Chapter 6 – Conceptual Ecological Model by Life Stage.....	33
BEVI Life Stage 1 – Nest.....	36
BEVI Life Stage 2 – Juvenile.....	43
BEVI Life Stage 3 – Breeding Adult.....	49
Chapter 7 – Causal Relationships Across All Life Stages.....	55
Anthropogenic Disturbance.....	56
Canopy Closure.....	56
Community Type.....	56
Diversity of Vegetation.....	57
Food Availability.....	58
Genetic Diversity and Infectious agents.....	58
Intermediate Structure.....	58
Local Hydrology.....	59
Matrix Community.....	60
Nest Predator and Cowbird Density.....	60
Patch Size.....	60
Predator Density.....	61
Stem Density.....	62
Chapter 8 – Discussion and Conclusions.....	63
Most Influential Activities and Processes Across All Life Stage.....	63
Potentially Pivotal Alterations to Habitat Elements.....	64
Gaps in Understanding.....	65

	Page
Literature Cited	69
Acknowledgments.....	81

Tables

Table		Page
ES-1	Outcomes of each of the three life stages of BEVI.....	3
1	BEVI life stages and outcomes in the LCR ecosystem.....	9
2	Distribution of BEVI critical biological activities and processes among life stages	11
3	Distribution of BEVI habitat elements and the critical biological activities and processes that they directly affect across all life stages	18
4	Habitat elements directly affected by controlling factors	27
5	Magnitude of influence of controlling factors on habitat elements	55

Figures

Figure		Page
1	Proposed BEVI life history model.....	10
2	Diagram conventions for LCR MSCP conceptual ecological models.	35
3	BEVI life stage 1 – nest, basic CEM diagram, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.....	39
4	BEVI life stage 1 – nest, high- and medium-magnitude relationships, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.	41
5	BEVI life stage 2 – juvenile, basic CEM diagram, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.....	45
6	BEVI life stage 2 – juvenile, high- and medium-magnitude relationships showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.	47

Figures (continued)

Figure		Page
7	BEVI life stage 3 – breeding adult, basic CEM diagram, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.....	51
8	BEVI life stage 3 – breeding adult, high- and medium-magnitude relationships, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.	53
9	Most influential biological activities and processes affecting each life stage of BEVI.	64
10	Habitat elements that directly or indirectly affect the most influential biological activities and processes across all life stages of BEVI. The legend is provided on figure 2.....	66

Attachments

Attachment

1	Species Conceptual Ecological Model Methodology for the Lower Colorado River Multi-Species Conservation Program
2	Arizona Bell’s Vireo Habitat Data

Foreword

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

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

- A synthesis of the current understanding of how a species’ habitat works. This synthesis can be based on the published literature, technical reports, or professional experience.
- Help in understanding and diagnosing underlying issues and identifying land management opportunities.
- A basis for isolating cause and effect and simplifying complex systems. These models also document the interaction among system drivers.
- A common (shared) framework or “mental picture” from which to develop management alternatives.
- A tool for making qualitative predictions of ecosystem responses to stewardship actions.
- A way to flag potential thresholds from which system responses may accelerate or follow potentially unexpected or divergent paths.
- A means by which to outline further restoration, research, and development and to assess different restoration scenarios.

- A means of identifying appropriate monitoring indicators and metrics.
- A basis for implementing adaptive management strategies.

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

Model building consists of determining system parts, identifying the relationships that link these parts, specifying the mechanisms by which the parts interact, identifying missing information, and exploring the model's behavior (Heemskerk et al. 2003¹). The model building process can be as informative as the model itself, as it reveals what is known and what is unknown about the connections and causalities in the systems under management.

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

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

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

The CEMs for species covered under the LCR MSCP are based on, and expand upon, methods developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): https://www.dfg.ca.gov/ERP/conceptual_models.asp. The ERP is jointly implemented by the California Department of Fish and Wildlife, U.S. Fish and Wildlife Service, and 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) 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 decisionmaking 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 Arizona Bell's vireo (*Vireo bellii arizonae*) (BEVI). The purpose of this model is to help the Bureau of Reclamation (Reclamation), Lower Colorado River Multi-Species Conservation Program (LCR MSCP), identify areas of scientific uncertainty concerning BEVI ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure BEVI habitat and population conditions. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read the attachment before continuing with this document.)

The identified research questions and gaps in scientific knowledge that are the result of this modeling effort serve as examples of topics the larger scientific community could explore to improve the overall understanding of the ecology of this species. These questions may or may not be relevant to the goals of the LCR MSCP. As such, they are not to be considered guidance for Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

CONCEPTUAL ECOLOGICAL MODELS

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

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

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

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

- **Life stages** – These consist of the major growth stages and critical events through which individual BEVI must pass in order to complete a full reproductive cycle.
- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals recruited to the next life stage or age class within a single life stage (recruitment rate), or the number of offspring produced (fertility rate).
- **Critical biological activities and processes** – These consist of activities in which the species engages and the biological processes that take place during each life stage that significantly beneficially or detrimentally shape the life-stage outcome rates for that life stage.
- **Habitat elements** – These consist of the specific habitat conditions, the abundance, spatial and temporal distributions, and other qualities that significantly beneficially or detrimentally affect the rates of the critical biological activities and processes for each life stage.
- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distributions, and qualities of the habitat elements for each life stage. Controlling factors are also called “drivers.”

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 change in the second condition. The CEM method applied here assesses four variables for each causal relationship: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the certainty of a present scientific understanding of the effect. CEM diagrams and a linked spreadsheet tool document all information on the model components and their causal relationships.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The BEVI conceptual ecological model addresses the BEVI throughout its breeding range. The model thus addresses the landscape as a whole rather than any single reach or managed area. The model does not address the biology of the BEVI during migration or in its winter range.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

The most widely used sources of the information for the BEVI conceptual ecological model are Reclamation (2008) and Kus et al. (2010). These publications summarize and cite large bodies of earlier studies. Where appropriate and accessible, those earlier studies are directly cited. The model also integrates numerous additional sources, particularly reports and articles completed since these publications; information on current research projects; and the expert knowledge of LCR MSCP biologists. Our purpose is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

The BEVI conceptual ecological model distinguishes and assesses three life stages and their associated outcomes as follows (table ES-1):

Table ES-1.—Outcomes of each of the three life stages of BEVI

Life stage	Life-stage outcome(s)
1. Nest	• Survival
2. Juvenile	• Survival
3. Breeding adult	• Survival • Reproduction

The model distinguishes 9 critical biological activities or processes relevant to 1 or more of these 3 life stages and their outcomes, 18 habitat elements relevant to 1 or more of these 9 critical biological activities or processes for 1 or more life stages, and 9 controlling factors that affect 1 or more of these 18 habitat elements. Because the lower Colorado River (LCR) and its refuges comprise a highly regulated system, the controlling factors almost exclusively concern human activities.

The nine critical biological activities and processes identified across all life stages are: disease, eating, foraging, molt, nest attendance, nest predation and brood parasitism, nest site selection, predation, and temperature regulation. The 18 habitat elements identified across all life stages are: anthropogenic disturbance, brood size, canopy closure, community type, diversity of vegetation, food availability, genetic diversity and infectious agents, intermediate structure, local hydrology, matrix community, nest predator and cowbird density, parental feeding behavior, parental nest attendance, patch size, predator density, previous year's use, stem density, and temperature. The nine controlling factors identified across all habitat elements are: fire management, grazing, mechanical thinning, natural thinning, nuisance species introduction and management, pesticide/herbicide application, planting regime, recreational activities, and water storage-delivery system design and operation.

RESULTS

The analysis of the causal relationships shows which critical biological activities and processes most strongly support or limit each life-stage outcome in the present system, which habitat elements most strongly affect the rates of these critical biological activities and processes, and which controlling factors most strongly affect the abundance, distribution, or condition of these habitat elements.

The analysis identifies several critical biological activities and processes that significantly affect survivorship across multiple life stages. Highlights of the results include the following:

- Predation and foraging (eating in the nest stage) are the most important critical biological activities and processes affecting survival of BEVI at all life stages. Other processes, such as disease, molt, and temperature regulation, can be very important, but are less understood, especially within the LCR.
- Only two processes directly affect reproduction—nest attendance (parental nest attendance) and nest site selection. Nest site selection is especially important, as it can indirectly influence survival of BEVI at all life stages. For example, good nest sites may have more food, fewer predators, and fewer diseases present.

Finally, the analysis highlights several potentially important causal relationships about which scientific understanding remains low. These may warrant attention to determine if improved understanding might provide additional management options for improving BEVI survivorship and recruitment along the LCR and its refuges. Specifically, the findings suggest a need to improve the understanding of the following:

(Note: Much data await analyses and may address some of the information gaps mentioned above [A. Leist 2015, personal communication]):

- Nest site selection is potentially affected by the most habitat variables, and much data have been collected along the LCR for BEVI (A. Leist 2015, personal communication). Pending data analyses will help clarify which habitat parameters (e.g., intermediate structure, patch size and other patch characteristics, humidity at the nest, etc.) are driving nest site selection along the LCR for this species. The effects of predator density and anthropogenic disturbance on nest site selection and nest attendance remain poorly understood for all bird species and have not been studied in BEVI.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

- The effects of disease, ecto-parasites, and endo-parasites have not been studied in BEVI or among passerine species inhabiting the LCR. Diseases have the potential to have dramatic impacts on populations (Robinson et al. 2010).
- What is the current level of cowbird parasitism of BEVI along the LCR? Are there other actions that need to be taken to improve nest success?
- BEVI exhibit site fidelity. Does this contribute to greater nest success?
- How important is canopy closure to BEVI in nest site selection, foraging, or other activities?
- What are the effects of anthropogenic disturbance on BEVI nest site selection and behavior, and what influences do different types of disturbances have on nesting success?
- How will climate change affect BEVI habitat vegetation phenology, nest site selection, and nest success? What management actions can be used to address this?
- Klicka et al. (2015) describe the first genetic analysis of the Bell's vireo across all its range in North America and recommend that that Bell's vireo should be divided into two species on an east/west divide, with the western species being named the least vireo (*Vireo pusillus*). They also support the idea of two subspecies for the western population. Additional genetic studies are needed to resolve the taxonomic status of the western subspecies (BEVI and least bell's vireo) and better assess their distributions and populations. This may also help clarify the potential for recolonization across the LCR in suitable habitats.
- How much do BEVI rely on matrix communities for foraging? What other influences do matrix communities and land management on these surrounding lands have on BEVI habitat use and reproductive success?

The research questions and gaps in scientific knowledge identified in this modeling effort serve as examples of topics the larger scientific community could explore to improve the overall understanding of the ecology of the BEVI. These questions 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.

Chapter 1 – Introduction

This document presents a conceptual ecological model (CEM) for the Arizona Bell's vireo (*Vireo bellii arizonae*) (BEVI). The purpose of this model is to help the Bureau of Reclamation (Reclamation), Lower Colorado River Multi-Species Conservation Program (LCR MSCP), identify areas of scientific uncertainty concerning BEVI ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure BEVI habitat and population conditions. The CEM methodology follows that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012), with modifications. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read the attachment before continuing with this document.)

The CEM addresses the BEVI population along the rivers and lakes of the lower Colorado River (LCR) and other protected areas along the LCR managed as BEVI habitat. The model thus addresses the landscape as a whole rather than any single reach or managed area.

The most widely used sources of information for the BEVI conceptual ecological model are Reclamation (2008) and Kus et al. (2010). These publications summarize and cite large bodies of earlier studies. Where appropriate and accessible, those earlier studies are directly cited. The CEM also integrates numerous additional sources, particularly reports and articles completed since the aforementioned publications; information on current research projects; and the expert knowledge of LCR MSCP biologists. The purpose of the conceptual model is not to provide an updated literature review but to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

This document is organized as follows: The remainder of chapter 1 provides a general description of the reproductive ecology of the Arizona bell's vireo, the purpose of the model, and introduces the underlying concepts and structure of the CEM. Succeeding chapters present and explain the model for the BEVI within the LCR and evaluate the implications of this information for management, monitoring, and research needs.

ARIZONA BELL'S VIREO REPRODUCTIVE ECOLOGY

Arizona Bell's vireos are considered complete migrants, breeding in North America and wintering in central and southern Mexico and Baja California

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

(Kus et al. 2010). Birds typically return to the LCR from their wintering grounds by late March to begin the breeding season. Kus et al. (2010) report that males arrive before females, often a few days to 2 weeks ahead. Scott (1888 in Bent 1950) reports that birds arrive already mated and immediately begin nest construction and egg laying.

Along the LCR, BEVI nest in riparian habitat, typically with willow [*Salix* sp.] and mesquite (*Prosopis* sp.) (Reclamation 2008). Male and female BEVI construct a loosely woven hanging nest in a “V” of a tree branch. Three to four eggs are laid, and both parents share incubation, which lasts about 14 days. Young birds fledge from the nest in 10–12 days, but fledglings remain in the vicinity of the nest, begging for food from their parents for 25–30 days. BEVI primarily feed on insects such as moths and their caterpillars (Lepidoptera), bugs (Hemiptera), and spiders (Aranea) (Bent 1950; Kus et al. 2010).

CONCEPTUAL ECOLOGICAL MODEL PURPOSES

Adaptive management of natural resources requires a framework to help managers understand the state of knowledge about how a resource “works,” what elements of the resource they can affect through management, and how the resource will likely respond to management actions. The “resource” may be a population, species, habitat, or ecological complex. The best such frameworks incorporate the combined knowledge of many professionals accumulated over years of investigations and management actions. CEMs capture and synthesize this knowledge (Fischenich 2008; DiGennaro et al. 2012).

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

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

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

A CEM thus translates existing knowledge into a set of explicit hypotheses. The scientific community may consider some of these hypotheses well tested, but others less so. Through the model, scientists and managers can identify which hypotheses, and the assumptions they express, most strongly influence management actions. The CEM thus helps guide management actions based on the results of monitoring and experimentation. These results indicate whether expectations about the results of management actions – as clearly stated in the CEM – have been met or not. Both expected and unexpected results allow managers to update the model, improving certainty about some aspects of the model while requiring changes to other aspects, to guide the next cycle of management actions and research. The CEM, through its successive iterations, becomes the record of improving knowledge and the ability to manage the system.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE FOR THE BEVI

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 Wildhaber et al. (2007), Wildhaber (2011), Kondolf et al. (2008), and Burke et al. (2009) 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 (Wildhaber et al. 2007; Wildhaber 2011). That is, it 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 typically include the number of individuals recruited to the next life stage (e.g., juvenile to adult) or next age class within a single life stage (recruitment rate), or the number of viable offspring produced (fertility rate). It then identifies the factors that shape the rates of these outcomes in the study area and thereby shapes the abundance, distribution, and persistence of the species in that area.

The BEVI 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.

Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River

- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals recruited to the next life stage (e.g., juvenile to adult), or 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 these five components and the causal relationships among them that affect life-stage outcome rates. Further, the CEM assesses each causal linkage based on four variables to the extent possible with the available information: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the status (certainty) of a present scientific understanding of the effect.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

The CEM for each life stage thus identifies the causal relationships that most strongly support or limit the rates of its life-stage outcomes, support or limit the rate of each critical biological activity or process, and support or limit the quality, abundance, and distribution of each habitat element (as these affect other habitat elements or affect critical biological activities or processes). In addition, the model for each life stage highlights areas of scientific uncertainty concerning these causal relationships, the effects of specific management actions aimed at these relationships, and the suitability of the methods used to measure habitat and population conditions. Attachment 1 provides further details on the assessment of causal relationships, including the use of diagrams and a spreadsheet tool to record the details of the CEM and summarize the findings.

Chapter 2 – BEVI Life Stage Model

A life stage consists of a biologically distinct portion of the life cycle 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 BEVI within the LCR on which to build the CEM.

INTRODUCTION TO THE BEVI LIFE CYCLE

In the development of the conceptual ecological model for the BEVI, we could not find a complete demographic study of the species. We therefore chose to represent the BEVI with a three-stage model to be consistent with other species documented within the LCR MSCP and to be most useful to management.

In many studies of avian demography, nest survival is considered integral in the reproduction of adults because adults are heavily invested in the care of eggs and nestlings (Etterson et al. 2011). We treat the nest stage as separate from adult reproduction due to the specific factors influencing the nest and the fit with the life-stage outcome modelling structure used in this CEM process.

We have chosen to combine the egg and nestling phases of development into a nest stage because the eggs and nestlings occupy the same nest; therefore, management focused on the nest will cover both eggs and nestlings. Further, most research conducted on BEVI breeding has focused on the number of young fledged and not on the number of eggs hatched—meaning that most of the available information is on the habitat characteristics and management actions associated with success of the nest through both the incubation and brooding periods.

The migratory nature of the BEVI complicates its management. The LCR MSCP is mainly responsible for management on the breeding grounds, and we therefore focus on three life stages occurring within LCR MSCP lands—nest, juvenile, and breeding adult. BEVI management during migration and winter, while certainly important, is outside of the scope of the LCR MSCP’s responsibilities.

BEVI LIFE STAGE 1 – NEST

The nest stage of the BEVI begins when the first egg is laid and ends either when the young fledge or the nest fails. Eggs are usually laid in April, and incubation lasts around 14 days (Bent 1950; Terres 1980), with all eggs in a clutch hatching

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

within 2 days of each other. Nestlings are generally present from mid-May into June (Reclamation 2008), and fledging usually occurs 10–12 days after hatching (Terres 1980; Kus et al. 2010).

The life-stage outcome from the nest stage is the survival of eggs and associated nestlings until fledging. It is important to note that the outcome of the nest stage is inherently tied to the behavior and condition of the parents.

BEVI LIFE STAGE 2 – JUVENILE

The juvenile stage begins at fledging and ends when the bird returns to the breeding grounds the next year. However, for the sake of this report, the influences are only evaluated through the bird's departure from the natal area on fall migration. For a few days after fledging, juveniles will remain close to the nest, within 5–10 meters (m) (Kus et al. 2010). Subsequently, juveniles will remain with parents for several weeks (25–30 days) and are fed by the parents during this time, although they can, and do, forage on their own (Kus et al. 2010). During fall migration, juveniles generally leave the breeding grounds 1 or 2 weeks after the adults, most leaving in late September or early October (Reclamation 2008; Kus et al. 2010). The life-stage outcome from the juvenile stage is the survival of the bird from fledging until its return to the breeding grounds the next calendar year. There are no studies available that analyze the juvenile survival rates in this species.

BEVI LIFE STAGE 3 – BREEDING ADULT

The adult stage begins when the bird returns to the breeding grounds after its first winter and ends when it departs the breeding grounds during fall migration, usually in late September. Generally, adults arrive on the breeding grounds in mid- to late March, with males arriving a few days to 2 weeks before females to set up territories (Reclamation 2008; Kus et al. 2010). Upon their return, females will choose a territory, and both males and females construct the nest, completing it over a 4- to 5-day period (Kus et al. 2010), although other citations (e.g., Bent 1950) specify that only females construct the nest. There are typically three to five eggs per clutch, and both the male and female incubate the eggs and care for the young (Bent 1950), although the female may do more than the male (Kus et al. 2010). BEVI pairs will re-nest after a failed attempt and may continue to re-nest (typically two to four times) until they are successful or the summer season ends (Kus et al. 2010). Most pairs are double brooded along the LCR (Franzreb 1989 and Brown 1993 in Kus et al. 2010).

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

The life-stage outcomes for breeding adults are survival and reproduction—here defined as the production of eggs. As noted earlier, most studies of bird demography define fecundity—or the reproductive rates of adults—as the number of offspring fledged (Etterson et al. 2011). We have separated the nest stage from adult fecundity to more clearly display the information regarding nest success so that it can be better assessed by management. Therefore, in this model, the fecundity of adults involves the acts of pairing, site selection, nest building, and the production of eggs.

It is important to note that the post-breeding period—after breeding but before migration—is a significant part of a bird's life cycle. Although males, females, and post-breeding individuals have different goals and responsibilities on the breeding grounds, we have included them all within the breeding adult life stage because their habitat use is similar, and thus, management directed at breeding adults will likely benefit all demographics present on the breeding grounds.

LIFE STAGE MODEL SUMMARY

Based on this information, the BEVI conceptual ecological model distinguishes three life stages and their associated life-stage outcomes as shown in table 1 and figure 1. The life stages are numbered sequentially beginning with the nest.

Table 1.—BEVI life stages and outcomes in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Nest	<ul style="list-style-type: none">• Survival
2. Juvenile	<ul style="list-style-type: none">• Survival
3. Breeding adult	<ul style="list-style-type: none">• Survival• Reproduction

Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River

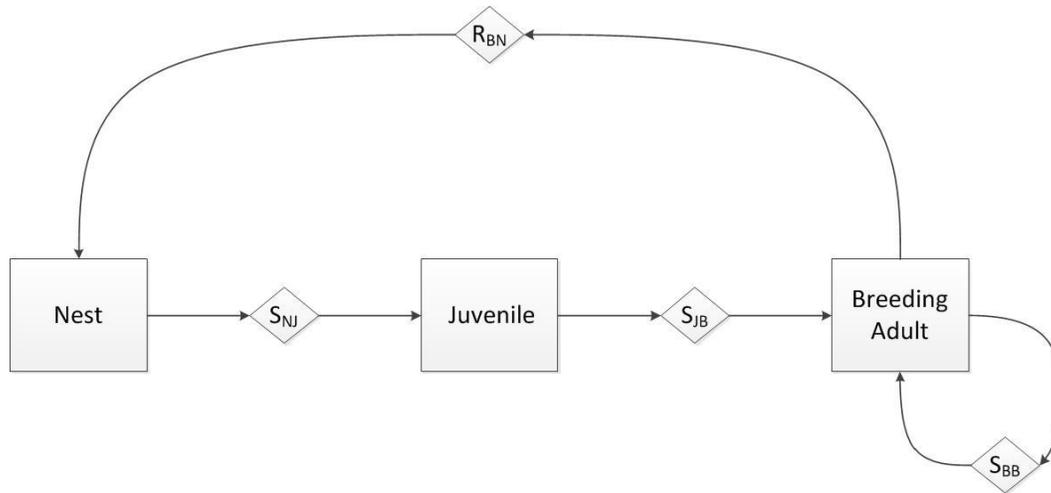


Figure 1.—Proposed BEVI life history model.

Squares indicate the life-stage, and diamonds indicate the life-stage outcomes.

S_{NJ} = survivorship rate, nest; S_{JB} = survivorship rate, juveniles; S_{BB} = survivorship rate, breeding adults; and R_{BN} = reproduction rate, breeding adults.

Chapter 3 – Critical Biological Activities and Processes

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

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

Table 2.—Distribution of BEVI critical biological activities and processes among life stages
(Xs indicate that the critical biological activity or process is applicable to that life stage.)

Life stage →			
	Nest	Juvenile	Breeding adult
Critical biological activity or process ↓			
Disease	X	X	X
Eating	X		
Foraging		X	X
Molt	X	X	X
Nest attendance			X
Nest predation and brood parasitism	X		
Nest site selection			X
Predation		X	X
Temperature regulation	X	X	X

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

The most widely used sources of the information used to identify the critical biological activities and processes are Reclamation (2008) and Kus et al. (2010). These publications summarize and cite large bodies of earlier studies. Where appropriate and accessible, those earlier studies are directly cited. The identification also integrates information from both older and more recent works as well as the expert knowledge of LCR MSCP biologists. The following paragraphs discuss the nine critical biological activities and processes in alphabetical order.

DISEASE

This process refers to diseases caused by infectious agents, including the effects of ecto- and endo-parasites. Disease prevalence and intensity can be influenced by a lack of genetic diversity. Little research has focused on specific diseases inflicting the BEVI; however, some mid-western populations of BEVI are known to be heavily parasitized by mites (e.g., northern fowl mite (*Ornithonyssus sylviarum*) (Kus et al. 2010), which may weaken nestlings and make them more susceptible to other parasites and diseases.

Although the more common avian diseases and parasites of North American birds are generally known (Morishita et al. 1999), some are often difficult to detect (Jarvi et al. 2002), and they can have differing effects on different species (Palinauskas et al. 2008). BEVI at all life stages are conceivably susceptible to disease. In addition, susceptibility to disease can be enhanced by other factors such as when ongoing stress from parental care weakens parental immune systems (Gill 2007).

EATING

This process only applies to the nest life stage because nestlings must eat to stay alive and develop but do not actively forage within their environment in the same way as juveniles and adults. A nestling's ability to eat during the first weeks of life is determined by the foraging and provisioning rate of its parents. (Juveniles are still fed by adults for some time after fledging – see the habitat element of “parental feeding behavior.”)

FORAGING

BEVI are predominantly insectivores, gleaning a variety of insects (and spiders) from all vegetation layers but mainly foraging in dense layers of vegetation within 4 m of the ground (Terres 1980; Kus et al. 2010). Both juveniles and adults

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

forage, but it is important to note that foraging by the parents affects the provisioning rate to nestlings and their parental care as well as supplemental feeding of juveniles.

MOLT

Nestling BEVI molt from natal down into juvenile plumage while in the nest. The success of this molt is dependent upon the adult provisioning rate (Howell 2010). Molting is an energetically costly process that may make nestlings more susceptible to death when resources are scarce (Howell 2010). In addition, juveniles and adults undergo post-juvenile and post-breeding molts, respectively, in July and August (Reclamation 2008).

NEST ATTENDANCE

Nestlings rely on the parents to provide food, protection from predators, and thermoregulation. In the case of BEVI, both males and females incubate eggs, brood young, and feed nestlings (Kus et al. 2010). Nest attendance is performed by breeding adults (and is dependent in part on their survivorship) and affects the nest life stage (egg hatching and provisioning rate to nestlings).

Nest attendance is affected by food availability. Research shows that nest attentiveness increases with food supplementation (Nilsson and Smith [1988] and Moreno [1989] in Theimer et al. 2011) such that an adult bird can spend more time at the nest caring for eggs or young if food is close by.

NEST PREDATION AND BROOD PARASITISM

Range-wide, nest predation is the primary threat to vireo nest success (Kus et al. 2010). Reported nest predators of least bell's vireo (*Vireo bellii pusillus*) in California include western scrub jay (*Aphelocoma californica*), Virginia opossum (*Didelphis virginiana*), gopher snake (*Pituophis melanoleucus*) and the Argentine ant (*Linepithema humile*) (Peterson et al. 2004). Other confirmed nest predators include, among others, domestic cats [*Felis catus*] and various snake species (e.g., black rat [*Pantherophis obsoletus*] and California kingsnake [*Lampropeltis getula californicae*]). Suspected nest predators include birds such as the American crow (*Corvus brachyrhynchos*) and greater roadrunner (*Geococcyx californianus*) along with mammals including the raccoon (*Procyon lotor*), coyote (*Canis latrans*), long-tailed weasel (*Mustela frenata*), and rodent species (Nolan 1960; Franzreb 1989; Collins et al. 1989 in Kus et al. 2010).

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

Nest parasitism by cowbirds (*Molothrus ater*) is also a major threat to BEVI (Kus et al. 2010), directly or indirectly affecting nest success. For example, brood parasitism accounted for about one-half of all nest failures along the Bill Williams River during the 1994 and 1995 nest seasons (Averill-Murray et al. 1999) and for 43 and 28% of nest failures in southeastern Arizona in 2006 and 2007, respectively (S. Steckler and C. Conway, personal communication *in* Kus et al. 2010). Kus and Whitfield (2005) and Laymon (1987) suggest that brood parasitism rates below 20–30% are necessary to maintain stable populations of vireos.

Adult vireos have different strategies and rates of success at deterring female cowbirds from depositing eggs in their nests. Initially, birds aggressively chase female cowbirds from the nest. However, if that doesn't work and if vireo clutch size declines significantly due to cowbird egg-laying activity, vireos will desert the parasitized nest and re-nest elsewhere (Kus et al. 2010). Burial of cowbird eggs deeper in the nest to prevent their incubation and hatching has also been noted as a strategy in areas outside Arizona (Kus et al. 2010).

These two processes (brood parasitism and nest predation) have been combined for the nest stage because (1) cowbirds are both nest predators and brood parasites (Theimer et al. 2011) and (2) habitat characteristics (distance to edge, patch width, etc.) affect both processes similarly.

NEST SITE SELECTION

Both breeding males and females select a nest site and construct the nest (Kus et al. 2010). Nest site selection affects vulnerability to predation and brood parasitism, environmental conditions at the nest, and foraging rates and, thus, is important for reproductive success (Saab 1999).

PREDATION

Predation is a threat to BEVI in all life stages, and it obviously affects survival. Predation on juveniles and adults is not as easily quantified, but it affects juveniles and adults directly and indirectly affects nest survival through abandonment. Predation risk (actual or perceived) can result in many behavioral responses in passerines, including changes in territory location, nest densities, altered clutch size, egg size, etc. (Lima 2009; Ghalambor and Martin 2002; Eggers et al. 2008; Theimer et al. 2011).

For this model, nest predation has been combined with brood parasitism and is treated as a separate critical biological activity and process at the nest life stage

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

(see above). Although there are few, if any, records in the literature of predation on adults, typical predators of adult birds likely include mammals and raptors such as falcons (*Falco* sp.) and accipiters (*Accipiter* sp.) (Kus et al. 2010). Kus et al. (2010) report a suspected incidence of a long-tailed weasel attack on a sleeping adult female least bell's vireo in the nest.

TEMPERATURE REGULATION

Temperature regulation is important for any organism inhabiting a region with temperatures as high as that of the LCR. Although overheating is possible during all life stages, most of the concern has been directed at eggs and nestlings (Rosenberg et al. 1991). Adults can affect the temperature regulation of eggs and nestlings through their own behavior (incubation, brooding, or shading) and through nest placement. Theimer et al. (2011) found that there was a temperature threshold that triggered changes in BEVI thermoregulatory behavior. Between 29 and 31 degrees Celsius (84–88 degrees Fahrenheit), parental behavior switched from brooding (to keep eggs warm) to shading eggs (to keep them cool) and from sitting tightly on the nest to standing over the nest and fanning with feathers.

Chapter 4 – Habitat Elements

Habitat elements consist of specific habitat conditions that ensure, allow, or interfere with critical biological activities and processes.

This chapter identifies 18 habitat elements that affect 1 or more critical biological activities or processes across the 3 BEVI life stages. Some of these habitat elements differ in their details among life stages. For example, BEVI at different life stages experience different predation risks. However, using the same labels for the same *kinds* of habitat elements across all life stages makes comparison and integration of the CEMs for the individual life stages across the entire life cycle less difficult.

The habitat elements included here were chosen based upon scientific literature demonstrating a direct influence on BEVI, influence on similar species or species in similar habitats, or based upon the experience of the author and reviewers with BEVI or related species.

Table 3 lists the 18 habitat elements and the critical biological activities and processes that they *directly* affect across all BEVI life stages.

The most widely used sources of the information used to identify the habitat elements are Reclamation (2008) and Kus et al. (2010). These publications summarize and cite large bodies of earlier studies. Where appropriate and accessible, those earlier studies are directly cited.

As with all tabulations of habitat associations, inferences that particular habitat characteristics are critical to a species or life stage require evidence and CEMs for why each association matters to species viability (Rosenfeld 2003; Rosenfeld and Hatfield 2006.)

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a one-to-three-word short name. However, each short name in fact refers to a longer, complete name. For example, “predator density” is the short name for “The abundance and distribution of predators that affect BEVI during the juvenile and adult stages.” The following paragraphs provide the full name for each habitat element and a detailed definition, addressing the elements in alphabetical order.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 3.—Distribution of BEVI habitat elements and the critical biological activities and processes that they directly affect across all life stages (Xs indicate that the habitat element is applicable to that critical biological activity or process.)

Critical biological activity or process →									
	Disease	Eating	Foraging	Molt	Nest attendance	Nest predation and brood parasitism	Nest site selection	Predation	Temperature regulation
Habitat element ↓									
Anthropogenic disturbance		X	X		X	X	X	X	
Brood size		X	X		X				
Canopy closure						X	X	X	X
Community type						X	X		
Diversity of vegetation			X				X		
Food availability			X		X		X		
Genetic diversity and infectious agents	X								
Intermediate structure							X		X
Local hydrology					X		X		X
Matrix community			X						
Nest predator and cowbird density						X			
Parental feeding behavior			X					X	
Parental nest attendance		X				X			X
Patch size							X		
Predator density					X		X	X	
Previous year's use							X		
Stem density						X	X	X	
Temperature					X		X		X

ANTHROPOGENIC DISTURBANCE

Full name: Human activity within or surrounding a given habitat patch, including noise, pollution, and other disturbances associated with human activity. Whether due to recreation, land management, or scientific research activities, the presence of humans can disturb BEVI, causing changes in behavior that might ultimately affect survival (Greaves 1989; Kus et al. 2008), although Brown (1993 in Kus et al. 2010) considers Bell's vireo to be relatively tolerant of anthropogenic disturbance. Most problematic would be disturbances during the

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

nesting season that would discourage nesting or cause nest abandonment. Barlow (1962 *in* Kus et al. 2010) reports premature fledging of nestlings in response to anthropogenic disturbance at the nest.

Anthropogenic disturbance can affect both breeding success and the survival of birds (reviewed by Barber et al. 2010; Francis and Barber 2013). Noise might mask conspecific cues such as songs or calls—making it more difficult for BEVI to attract or find mates or defend territories. Noise may also affect foraging, eating, nest attendance, predation rates, etc. (Ware et al. 2015). Anthropogenic disturbance effects have not been thoroughly studied in BEVI or within the LCR, so specific impacts are not quantified. Barrett (1996 *in* Barrett 1997) reports on U.S. Fish and Wildlife Service (USFWS) recommendations to avoid traffic or construction noise levels above 60 decibels near nesting least bell's vireos, although the biological validity of this number has been questioned. Anthropogenic disturbance is considered to be a habitat element, as it is an environmental characteristic with which a nesting or foraging vireo must contend.

BROOD SIZE

Full name: **The number of young in the nest.** This element refers to the number of young that the parents must rear. Brood size is related to maternal health, and the well-being of both parents depends in part on the availability of sufficient food resources in close proximity to the breeding territory as well as other factors such as predator density (see “Nest Predator and Cowbird Density”). The typical brood consists of three to four young (Kus et al. 2010).

CANOPY CLOSURE

Full name: **The proportion of the sky hemisphere obscured by vegetation when viewed from a single point as measured with a spherical densitometer (Jennings et al. 1999).** This element refers to the percent closure of canopy vegetation in the vicinity of the BEVI nest site. The Great Basin Bird Observatory (GBBO) (2011) found that BEVI territories were placed in sites with significantly greater canopy cover than non-use sites. However, tree overstory in vireo habitat is often more patchy or open when compared with other riparian nesting birds, as vireos are typically selecting early successional habitat with a dense shrub layer (understory).

Canopy cover may affect the availability of food (Smith et al. 2006) in part by modifying moisture levels in the habitat patch; moisture levels have been identified as important to arthropod abundance (Allen 2016). Tree canopies and shade also moderate temperatures in a vegetation patch (Thelander and

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

Crabtree 1994). The importance of canopy closure to BEVI is not clear, but ongoing research is underway to better understand this relationship (A. Leist 2015, personal communication).

COMMUNITY TYPE

Full name: The species composition of the riparian forest patch. This element refers to the species composition of riparian habitat used for breeding by BEVI. In the Southwest, Bell's vireos typically breed in cottonwood (*Populus fremontii*)-willow riparian forest, with mesquite or seep-willow (*Baccharis salicifolia*) understory shrubs (Grinnell 1914; Kus et al. 2010; GBBO 2011). BEVI territories along the LCR had significantly less upland vegetation than non-use sites (A. Leist 2015, personal communication). Bell's vireos occasionally use salt cedar (*Tamarix* sp.) – in fact, 52% of the nests along the LCR (Averill-Murray et al. 1999) and 64% of the nests in the Grand Canyon were in salt cedar (Brown 1993 in Kus et al. 2010). A mixed salt cedar/honey mesquite (*Prosopis glandulosa*) community is found at a number of LCR sites. Phenology of the mesquite and catclaw (*Acacia greggii*) on LCR sites is also important for migration, arrival on the LCR, and nest initiation of BEVI (McGrath et al. 2009; A. Leist 2015, personal communication).

In addition to nest site selection, community type also affects invertebrate diversity and nutrient content (Wiesenborn 2014).

DIVERSITY OF VEGETATION

Full name: Either horizontal or vertical diversity of the vegetation structure at the patch or microhabitat scales or diversity of community types or ages at the landscape scale. The diversity of vegetation affects site use by many animals (MacArthur and MacArthur 1961; Erdelen 1984; Wiens et al. 1993). BEVI prefer nest sites with low, dense shrub cover (predominantly native willows), often near the edge of a thicket or woodland, generally habitats typical of early successional stages (Kus et al. 2010). At the Bill Williams River National Wildlife Refuge (Bill Williams River NWR), BEVI use mostly edges (mesquite and catclaw habitat) that do not have an overstory component (A. Leist 2015, personal communication).

Horizontal heterogeneity of vegetation within a territory or patch is also important for site use of BEVI. Nests are often placed in low shrubs near small openings under the canopy (Franzreb 1989) at the edge of a patch of vegetation. Dense areas provide vegetation to conceal nests and provide microclimate needed for egg and nestling development. At the Bill Williams NWR, BEVI that nest in

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

interior habitats select those whose interiors mostly have open spaces, such as washes or edges (A. Leist 2015, personal communication). Although proximity to open areas may increase vulnerability to nest predators, brood parasites, or predation in general, it may also facilitate foraging. In fact, GBBO biologists have observed BEVI foraging in open areas when provisioning nestlings and fledglings (A. Leist 2015, personal communication).

FOOD AVAILABILITY

Full name: **The abundance of food available for adults and their young.** This element refers to the taxonomic and size composition of the invertebrates that an individual BEVI will encounter during each life stage as well as the density and spatial distribution of the food supply in proximity to the nest. BEVI are primarily insectivores during the breeding season, feeding on insects and spiders predominantly (Kus et al. 2010). The abundance and condition of the food supply affects adult health (and subsequent reproductive output) as well as the growth and development of the young during the nestling and juvenile stages. Stomach analyses conducted by Chapin (1925 in Bent 1950) showed that most insects consumed were bugs, beetles (Coleoptera), caterpillars, and grasshoppers (Orthoptera), though in midsummer they occasionally will eat fruits and/or vegetable matter. More recent work by Yard et al. (2004) confirms a similar diet for breeding Arizona bell's vireos, with the addition of some flies and aquatic midges (Diptera) and spiders.

GENETIC DIVERSITY AND INFECTIOUS AGENTS

Full name: **The genetic diversity of BEVI individuals and the types, abundance, and distribution of infectious agents and their vectors.** The genetic diversity component of this element refers to the genetic homogeneity versus heterogeneity of a population during each life stage. The greater the heterogeneity, the greater the possibility that individuals of a given life stage will have genetically encoded abilities to survive their encounters with the diverse stresses presented by their environment and/or take advantage of the opportunities presented (Allendorf and Leary 1986). Franzreb (1989) reports that habitat fragmentation not only increases cowbird parasitism rates, it separates vireos into distinct subpopulations more susceptible to local extinction (see Kus et al. 2010). GBBO (2012) also acknowledges the importance of connectivity among subpopulations to stability in vireo populations.

Klicka et al. (2015) describe the first genetic analysis of the Bell's vireo across its range in North America and recommend that the Bell's vireo should be divided into two species on an east/west divide, with the western species being named the least vireo (*Vireo pusillus*). They also support the idea of two subspecies for the

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

western population. Additional genetic studies are needed to resolve the taxonomic status of the western subspecies (BEVI and least bell's vireo) and better assess their distributions. They did find what is currently known as the least Bell's vireo (federally endangered subspecies) in California very near the border with Nevada and not far from the LCR.

The infectious agent component of this element refers to the spectrum of viruses, bacteria, fungi, and parasites that individual BEVI are likely to encounter during each life stage. The effects of disease and other infectious agents are poorly understood. Although the more common avian diseases and parasites of North American birds are generally known (Morishita et al. 1999), some are often difficult to detect (Jarvi et al. 2002), and they can have differing effects on different species (Palinauskas et al. 2008). BEVI at all life stages are conceivably susceptible to disease.

INTERMEDIATE STRUCTURE

Full name: **The concealment provided by the vegetation structure between the canopy and the herbaceous (=ground) layer.** This element refers to the visual density of vegetation (i.e., concealment) below the uppermost canopy layer to the ground. Dense understory vegetation (a shrub layer up to 3 m high) is characteristic of least bell's vireo nesting habitat (Goldwasser 1981; Franzreb 1989; Kus et al. 2010) and is one of the most often-listed characteristics of BEVI habitat (B. Sabin and A. Leist 2015, personal communication). Studies in LCR from 2008–10 showed that BEVI selected denser vegetation (based on densitometer readings) for nesting (A. Leist 2015, personal communication). A more dense understory may support a more diverse and abundant invertebrate food supply as well as provide protection or concealment from predators and cowbird parasitism (Budnik et al. 2002; Kus et al. 2010).

LOCAL HYDROLOGY

Full name: **Aspects such as the distance to standing water or the presence of adjacent water bodies, timing and volume of floods, depth to the water table, and soil moisture levels.** This element refers to anything that affects soil moisture, such as the proximity of water to the nesting habitat, elevation, irrigation practices, and soil texture. The local hydrological conditions of a given patch are an important determinant of BEVI habitat quality in riparian areas because it affects other aspects of habitat such as vegetation structure, cottonwood recruitment, and abundance of the arthropods (Ahlers and Moore 2009; Burke et al. 2009). Wetter conditions might also provide cooler temperatures and higher overall humidity necessary for egg and chick survival, generally, in these desert

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

systems (Rosenberg et al. 1991; McLeod and Pellegrini 2013). BEVI may benefit similarly from higher humidity levels in dense vegetation; Reclamation data analyses may further clarify this in future years (B. Sabin 2015, personal communication). Additionally, local hydrology can also affect prey composition and overall food abundance (Ellis et al. 2001).

Vireo nests have been measured at occurring less than 1,000 m from water in California sites with the presence of ponded surface water (either perennial or intermittent water) (Averill-Murray and Corman 2005 *in* Kus et al. 2010) or moist soil considered important features of vireo nesting habitat (Barlow 1962 *in* Kus et al. 2010; USFWS 1986; Rosenberg et al. 1991). GBBO (2010) also found a strong association between BEVI territory location and proximity of surface water at selected LCR sites. In particular, they are found along the Virgin River and the edges of Lakes Mead, Mohave, and Havasu. At the Bill Williams River NWR, they nest near areas where surface water is present at various times during the year (A. Leist 2015, personal communication).

MATRIX COMMUNITY

Full name: **The type of habitat surrounding riparian patches used by vireos.** This element refers to the types of plant communities and land-use activities surrounding the riparian habitat patches used by BEVI. Least bell's vireo forage in upland vegetation next to riparian corridors (Salata 1983 *in* Kus et al. 2010); therefore, the matrix community may affect foraging of BEVI if habitat is suitable.

In California, researchers found that least bell's vireo territories surrounded by agriculture and urban development produced fewer young than did territories bordering on native vegetation. This was likely due to the increased nest parasitism by cowbirds that benefitted from the fragmentation of the modified matrix habitat (RECON *in* Kus 2002).

Work by Kus et al. (2008), looking at factors affecting nest survival in least bell's vireo populations in California, found that factors at the landscape scale, not the fine or intermediate scale, were most important determinants of survival. Specifically, the proximity to golf courses increased the odds of predation, while the proximity to natural, wetland habitat decreased the odds of predation, supporting the idea that the matrix community does have an effect on bell's vireos and factors affecting their habitat use and nest success.

NEST PREDATOR AND COWBIRD DENSITY

Full name: **The abundance and distribution of nest predators and brood parasites.** This element refers to a set of closely related variables that affect the likelihood that different kinds of predators will encounter and successfully prey on BEVI during the nest life stage or cowbirds or other nest parasites will lay eggs in the nest. The variables of this element include the species and size of the fauna that prey on BEVI during different life stages, the density and spatial distribution of these fauna in the riparian habitat used by vireos, and the ways in which predator activity may vary in relation to other factors (e.g., time of day, patch size and width, matrix community type, etc.) (Thompson, III 2007). Documented nest predators of least bell's vireo in California include western scrub jay, Virginia opossum, gopher snake, and the Argentine ant (Peterson et al. 2004). See the critical biological activity and process of "nest predation and brood parasitism" for additional lists of predators.

For open cup nesters like BEVI, nest predation has been identified as a major factor affecting annual productivity (Ricklefs 1969; Martin 1988).

PATCH SIZE

Full name: **The size and shape (including width) of riparian habitat patches.** This element refers to the areal extent of a given patch of riparian vegetation. Patch size and shape affects the number of breeding pairs that an area can support as well as the density of predators, competitors, and brood parasites. Various studies of least bell's vireo have shown that vireos were more abundant and reproduced more successfully in larger cottonwood-willow habitat patches (e.g., 160-hectare sites in Lower Colorado River Valley) (Lynn 1996 *in* Kus et al. 2010). Brown (1993 *in* Kus et al. 2010) estimates an average territory size for least bell's vireo to be 0.7 hectare in size; other estimates for least bell's vireo in California are similar (see Kus et al. 2010 and references therein). Additionally, Grinnell (1914) observed BEVI defending linear territories approximately 183 m in length along riparian corridors along the Bill Williams River.

Little solid information is available about the importance of patch size to BEVI occupancy, but we suspect that it plays a role in nest site selection. Narrow linear patches may be less acceptable to birds than wider ones, as width may also affect the presence of nest parasites and other predators. Research by Kus et al. (2008) on least bell's vireo did not find any significant reduction in predation levels with increased distance from habitat edges; however, it is unclear as to whether this is

due to the fact that all the habitat she studied was, in fact, edge habitat (being narrow riparian corridor). There are no data currently on patch width as it affects BEVI.

PARENTAL FEEDING BEHAVIOR

Full name: **The ability and behavior of parents to feed and care for juveniles after they fledge from the nest.** This element refers to the capacity of both parents to provision food for recently fledged birds. BEVI parents have been reported to provide some food to their young for 25–30 days after fledging (NatureServe 2015), although fledged juveniles also forage on their own (Kus et al. 2010). The feeding rate is dependent upon food availability and the number of young in the brood. This rate influences the amount of food and the time spent foraging by juvenile birds.

PARENTAL NEST ATTENDANCE

Full name: **The ability of both parents to care for young during the egg/incubation and nestling stages.** This element refers to the capacity of both parents to share nesting and brood rearing responsibilities until fledging. It is affected primarily by the presence of predators and food availability.

PREDATOR DENSITY

Full name: **The abundance and distribution of predators that affect BEVI during juvenile and adult stages.** This element refers to a set of closely related variables that affect the likelihood that different kinds of predators will encounter and successfully prey on BEVI during the juvenile or adult life stages. The variables of this element include the species and size of the fauna that prey on BEVI during these life stages, the density and spatial distribution of such predators in the riparian habitat used by BEVI, and whether predator activity may vary in relation to other factors (e.g., time of day, patch size and width, matrix community type, etc.) (Thompson, III 2007). For example, mesopredator release coupled with the introduction of new predators (e.g., domestic and feral [*Felis silvestris catus*] cats) in more urban developments around riparian habitat may be contributing to increases in predator density in least bell's vireo habitat in California (USFWS 2006). Apart from direct effects on BEVI survival, predator density also can alter parental care behavior, nest site selection, and foraging activity (Lima 1998, 2009; Chalfoun and Martin 2009).

PREVIOUS YEAR'S USE

Full name: **The location of the previous year's breeding attempt (and whether or not that attempt was successful).** Bell's vireos typically return to the same nesting territory year after year (Greaves 1989; Franzreb 1989 *in* Kus et al. 2010). Fledglings also return to their natal area to breed (Greaves and Gray 1991). It is not known whether this is due to site fidelity, whether these territories simply have the best microhabitat for nesting, or whether there are other cues that trigger nesting (Kus et al. 2010). Whether this tendency to return to the same habitat to breed contributes to greater BEVI nest success, as has been demonstrated with the southwestern willow flycatcher (Paxton et al. 2007; McLeod and Pellegrini 2013) is not known.

STEM DENSITY

Full name: **The stem density of trees and shrubs greater than 2.5 centimeters in diameter.** This element refers to the number of trees and/or shrubs per acre of that size or larger. The greater the tree and/or shrub density, the greater the likelihood of denser vegetative cover. Stem density can be correlated with tree canopy cover, intermediate structure, and total vegetation density (see "Diversity of Vegetation," above). Stem data collected from 2011–14 at selected LCR sites are awaiting analyses (A. Leist 2015, personal communication).

TEMPERATURE

Full name: **The mean temperature in a habitat patch or nest site.** This element refers to the average temperature in the nesting habitat around the nest site (or during the nesting season). High temperatures typical of the LCR region in summer can kill eggs and stress young in the nest (Hunter et al. 1987; Rosenberg et al. 1991). Mean nest site temperature data are awaiting analyses (A. Leist and B. Sabin 2015, personal communication).

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics, both natural and anthropogenic, which affect the abundance, spatial and temporal distributions, and quality of critical habitat elements. These may also significantly directly affect some critical biological activities or processes. A hierarchy of such factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on nine immediate controlling factors that are within the scope of potential human manipulation. The nine controlling factors identified in this CEM do not constitute individual variables; rather, each identifies a category of variables (including human activities) that share specific features that make it useful to treat them together. Table 4 lists the nine controlling factors and the habitat elements they directly affect. Table 4 also shows five habitat elements that are not directly affected by any controlling factor (brood size, parental feeding behavior, parental nest attendance, previous year’s use, and temperature). These latter habitat elements are directly shaped by the condition of one or more other habitat elements rather than by any of the controlling factors.

Table 4.—Habitat elements directly affected by controlling factors

Controlling factor →									
Habitat element ↓	Fire management	Grazing	Mechanical thinning	Natural thinning	Nuisance species introduction and management	Pesticide/herbicide application	Planting regime	Recreational activities	Water storage-delivery system design and operation
Anthropogenic disturbance			X					X	
Brood size	N/A*								
Canopy closure	X		X	X			X		
Community type	X	X			X		X	X	
Diversity of vegetation	X	X						X	
Food availability					X	X			
Genetic diversity and infectious agents									X
Intermediate structure	X	X	X		X		X	X	
Local hydrology									X
Matrix community	X	X					X		
Nest predator and cowbird density					X			X	
Parental feeding behavior	N/A*								
Parental nest attendance	N/A*								
Patch size	X	X					X	X	
Predator density					X			X	
Previous year’s use	N/A*								
Stem density	X	X	X	X			X	X	
Temperature	N/A*								

N/A values suggest that none of the identified controlling factors *directly* affect the habitat element.

FIRE MANAGEMENT

This factor addresses any fire management (whether prescribed fire or fire suppression) that could affect BEVI or their habitat. Effects may include creation of habitat that supports or excludes BEVI, a reduction in the food supply of invertebrates, or support of species that pose threats to BEVI as predators, competitors, or carriers of infectious agents. Although typically not a major threat in most riparian habitats, severe wildfires have affected southwestern willow flycatcher breeding sites in the past decade (USFWS 2002; Graber et al. 2007; Ellis et al. 2008) and could affect BEVI riparian habitats, similarly. In fact, severe fires have recently occurred in a few LCR restoration sites (Hunters Hole and Yuma East Wetlands) and in riparian habitat at the Havasu National Wildlife Refuge (C. Dodge 2015, personal communication). Climate change is also projected to affect fire frequency along the LCR (USFWS 2013), in part by altering rainfall patterns, etc.

GRAZING

This factor addresses the grazing activity on riparian habitats along the LCR and in surrounding areas that could affect BEVI or their habitat. Grazing by cattle (Bovidae), burros (*Equus asinus*), or mule deer (*Odocoileus hemionus*) across the arid Southwestern United States has substantially degraded riparian habitat (see Appendix G in USFWS 2002). (Note: Reclamation staff and researchers have observed mule deer browsing on LCR sites, which may become an issue if populations are not managed). Grazing may thin the understory or even prevent the establishment of cottonwood and willow seedlings (Kauffman et al. 1997). In particular, overgrazing has been identified as a management issue along the San Pedro River and the Verde River (S. Kokos 2014, personal communication). Krueper (1993) and Krueper et al. (2003) report that fencing cattle out of sensitive riparian habitats in the San Pedro Riparian National Conservation Area led to improved habitat quality and increased riparian bird density within 4 years. Livestock grazing is also known to occur at the Gila River study area (Graber et al. 2012).

Feral pigs (*Sus scrofa*) have been identified as a problem for least bell's vireos in California's Santa Ana River watershed habitat but, although present on the Havasu National Wildlife Refuge, they have not been found to adversely affect BEVI there and are not found farther south along the LCR (C. Dodge 2015, personal communication).

MECHANICAL THINNING

This factor addresses the active removal of vegetation from areas within the LCR region. Effects may include creation of habitat that supports or excludes BEVI or supports or excludes species that pose threats to BEVI such as predators, competitors, or carriers of infectious agents. This factor includes the thinning of vegetation within both riparian and matrix communities. Thinning can be implemented on a small, local scale, resembling natural thinning, or can be implemented on a broad scale with larger and more complete transition.

NATURAL THINNING

This factor addresses the natural death of trees within a patch of riparian forest or the surrounding matrix. As overstory trees die, they leave openings in the canopy, thereby allowing light to reach lower vegetation layers and creating the horizontal and vertical foliage profiles preferred by BEVI as shrubby vegetation fills in the gaps. This structural complexity may increase food availability.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

This factor addresses the intentional or unintentional introduction of nuisance species (animals and plants) and their control that affects BEVI survival and reproduction. The nuisance species may infect, prey on, compete with, or present alternative food resources for BEVI during one or more life stages; cause other alterations to the riparian food web that affect BEVI; or affect physical habitat features such as canopy or shrub cover. For example, cowbird control has successfully reduced parasitism rates in many bell's vireo populations (Averill-Murray et al. 1999; Morrison and Averill-Murray 2002; Kus and Whitfield 2005; and Kus et al. 2010). Removal of an invasive plant species, giant reed grass (*Arundo donax*), has helped re-establish native riparian vegetation at certain California sites, which have subsequently been used by least bell's vireos.

BEVI will successfully nest in salt cedar. The complicated nature of the relationship between salt cedar and BEVI is highlighted by another introduced species—the tamarisk beetle (*Diorhabda* spp.). The tamarisk beetle was introduced into the LCR region in order to control invasive salt cedar (Bateman et al. 2013). However, defoliation of salt cedar due to beetle infestation causes decreases in humidity and cover along with increases in temperature (Bateman et al. 2013), thereby degrading areas dominated by salt cedar as habitat for BEVI.

PESTICIDE/HERBICIDE APPLICATION

This factor addresses pesticide/herbicide applications that may occur on or adjacent to riparian habitat of the LCR region. Pesticides/herbicides may drift into riparian areas, removing plant species important to BEVI habitat structure and composition. Pesticide/herbicide effects may include sublethal poisoning of BEVI via ingestion of treated insects, pollution of runoff into wetland habitats that are toxic to prey of BEVI, and a reduced invertebrate food supply.

PLANTING REGIME

This factor addresses the active program to restore cottonwood-willow riparian habitat along the LCR and includes both the community planted as well as the manner in which it is planted within restoration areas (e.g., density, age, and patch size). The composition of the species planted can affect not only the vertical and horizontal structure of the vegetation but also the insect community within a given patch (Bangert et al. 2013; Wiensenborn 2014).

Although BEVI use a variety of habitats, the Bell's vireo can use similar habitat components as the southwestern willow flycatcher and, therefore, may respond positively to habitat management for the southwestern willow flycatcher in low elevation riparian habitat, especially if there is a dense shrub layer (Latta et al. 1999). In addition, habitat restoration for least bell's vireo in California by planting cuttings of riparian species has been successful at attracting the vireos to nest (Kus 1998; Howell and Dettling 2009). Successful vireo nesting was reported within 3–5 years after restoration in sites with a dense understory within 0.9 m of the ground and proximity to some water (Baird and Reiger 1989; Kus 1998). In the Bill Williams River NWR, BEVI have been found in restoration sites older than 2 years (GBBO 2010).

RECREATIONAL ACTIVITIES

This factor addresses the disturbance to BEVI from recreational and research activities. Even non-consumptive human activity can have negative effects on wildlife (reviewed by Boyle and Samson 1985). This is a broad category that encompasses the types of recreational activities (e.g., boating, fishing, horseback riding, camping, and off-road vehicle [ORV] use) as well as the frequency and intensity of those activities. The impacts may consist of disturbance and habitat alteration. Recreational activities can influence nest predator densities by either increasing predator success rates through interfering with or distracting prey or by decreasing predator success rates through interfering with or distracting the predator, (Mason 2015; Ware et al. 2015).

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

ORVs have been identified as a threat to least bell's vireo in the Santa Ana watershed, California, mainly due to effects on riparian nesting habitat. Such effects may include tramping, clearing of vegetation, woodcutting, prevention of seedling germination due to soil compaction, among other effects (USFWS 2002). Additionally, intensive research and monitoring that regularly disturbs nesting birds may adversely affect nest success. The impacts will depend on the tolerance of the bird species in question, predators and brood parasites present in the habitat, the frequency and type of nest disturbance, and other factors. However, precautionary measures should be included in the design of monitoring protocols until more is known about the potential effects of research-related disturbance on nesting BEVI.

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATION

Much of the habitat currently used by BEVI within the LCR area is along regulated waterways. The water moving through this system is highly regulated/managed for storage and delivery (diversion) to numerous international, Federal, State, Tribal, and municipal users and for hydropower generation.

This factor includes river and off-channel water management, including pumping of groundwater and diversion of river water to manage water levels in refuge ponds as well as dewatering and flushing of marsh habitats. The amount of water, flooding frequency, water depth and stability, etc., each affect the local hydrology and therefore the species composition and density of the riparian plant community favored by BEVI for food, shelter, and nesting. Large-scale water releases in spring can flood low-lying BEVI nests in downstream areas (Brown and Johnson 1985 *in* Kus et al. 2010). Dam and reservoir construction projects also destroy and separate riparian habitat patches, which may affect the genetic makeup of BEVI populations (Franzreb 1989 *in* Kus et al. 2010). In contrast, management of water levels at Glen Canyon Dam added riparian habitat in the Grand Canyon for BEVI (Brown and Johnson 1985 *in* Kus et al. 2010). Generally, the dynamic nature of a free-flowing river creates a mosaic of riparian habitats, and thus, a natural flow regime should be beneficial to BEVI.

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains three sections, each presenting the CEM for a single BEVI life stage. The text and diagrams identify the critical biological activities and processes for each life stage, the habitat elements that support or limit the success of these critical biological activities and processes, the controlling factors that determine the abundance and quality of these habitat elements, and the causal links among them. The CEM sections specifically refer to conservation and other protected areas managed as BEVI habitat and thus addresses this landscape as a whole rather than any single reach or managed area.

The CEM 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

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

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."

The CEM for each life stage thus identifies 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.

A separate spreadsheet is used to record the assessment of the character and direction, magnitude, predictability, and scientific understanding for each causal link along with the underlying rationale and citations for each life stage. The CEM for each life stage, as cataloged in its spreadsheet, is illustrated with diagrams showing the controlling factors, habitat elements, critical biological activities and processes, and causal links identified for that life stage. A diagram may also visually display information on the character and direction, magnitude, predictability, and/or 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.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

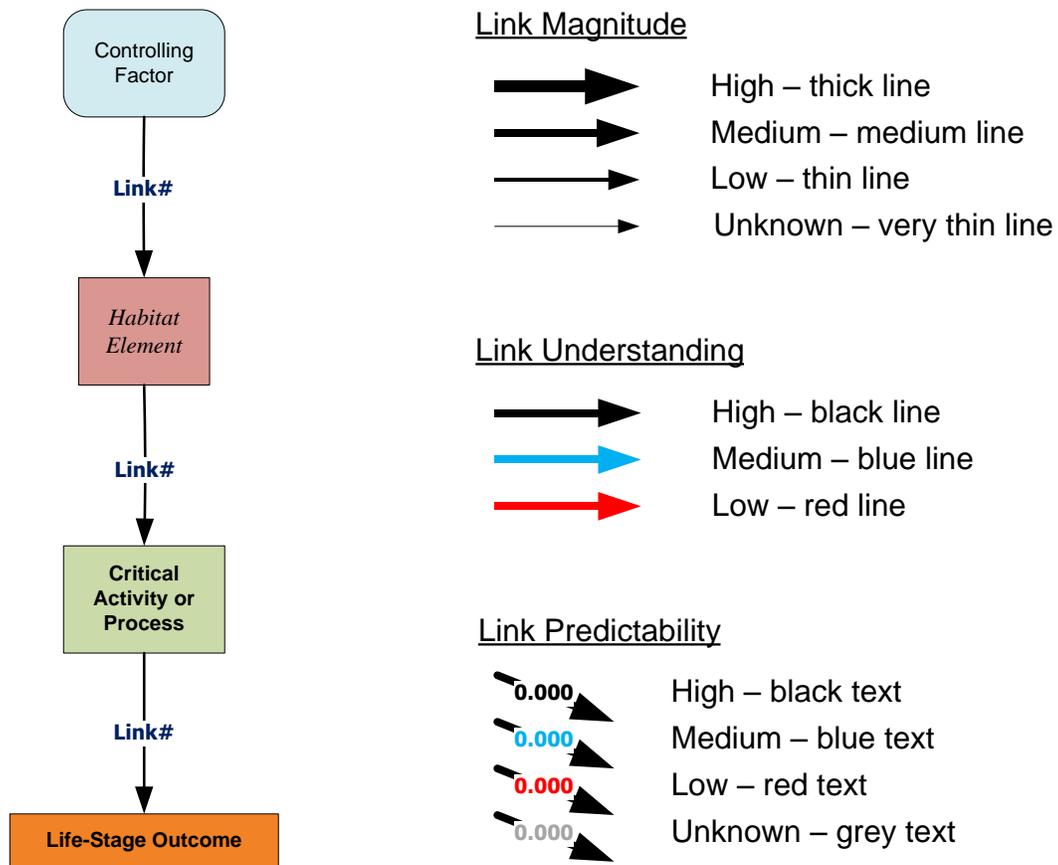


Figure 2.—Diagram conventions for LCR MSCP conceptual ecological models.

The discussion of each life stage includes an analysis of the information contained in the spreadsheet. The analyses highlight causal chains that strongly affect survivorship, identify important causal relationships with different levels of predictability, and identify important causal relationships with high scientific uncertainty. The latter constitutes topics of potential importance for adaptive management investigation.

The causal relationships between controlling factors and habitat elements are essentially identical across all three life stages. For this reason, the discussion of controlling factor-habitat element linkages across all three life stages appears in a subsequent chapter.

BEVI LIFE STAGE 1 – NEST

The nest stage lasts from when the egg is laid until either the young fledge or the nest fails. Success during this life stage – successful transition to the juvenile stage – involves organism survival, maturation, molt, and fledging. The organisms actively interact with their environment.

The CEM (figures 3 and 4) recognizes five (of nine) critical biological activities and processes for this life stage. Foraging, nest attendance, nest site selection, and predation are not included, as they are activities and processes of other life stages. The critical biological activities and processes are presented here, ordered as they appear on the following figures.

1. **Disease** – Although the literature does not emphasize disease as affecting population levels of BEVI, we still feel that disease bears mentioning. Diseases and parasites are prevalent in avian populations, so it is safe to assume they have an impact on BEVI (Morishita et al. 1999; Lachish et al. 2011). Disease and parasite impacts along the LCR is recommended as an area of potential research.

The CEM recognizes genetic diversity and infectious agents as a habitat element affecting disease.

2. **Eating** – The nestling must eat to maintain metabolic processes and relies on the parent to provide food, protection from predators, and thermoregulation.

The CEM recognizes brood size and parental nest attendance and as habitat elements directly affecting eating.

3. **Nest Predation and Brood Parasitism** – Nest predation and brood parasitism affect the survival of nestlings.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, nest predator and cowbird density, parental nest attendance, and stem density as habitat elements affecting nest predation.

4. **Molt** – The nestling must molt into juvenile plumage, which directly affects survival.

The CEM does not recognize any habitat elements as directly affecting molt. Other critical biological activities and processes influencing molt include eating and disease.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

5. **Temperature Regulation** – The eggs and nestlings must maintain an optimum temperature to develop and survive.

The CEM recognizes canopy closure, intermediate structure, local hydrology, parental nest attendance, and temperature as the primary habitat elements directly affecting temperature regulation. The critical biological process and activity of disease can also influence temperature regulation.

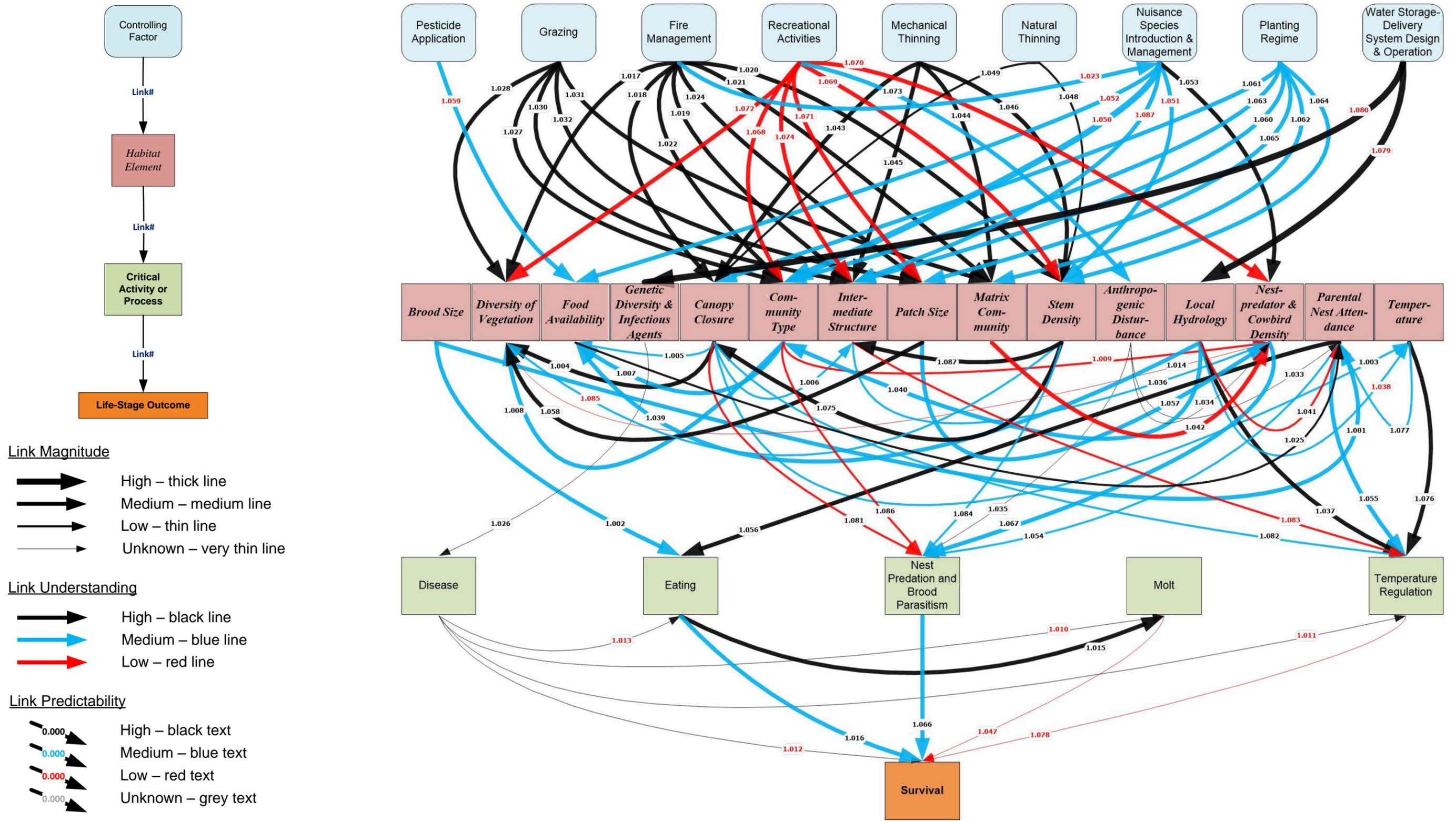


Figure 3.—BEVI life stage 1 – nest, basic CEM diagram, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.

Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River

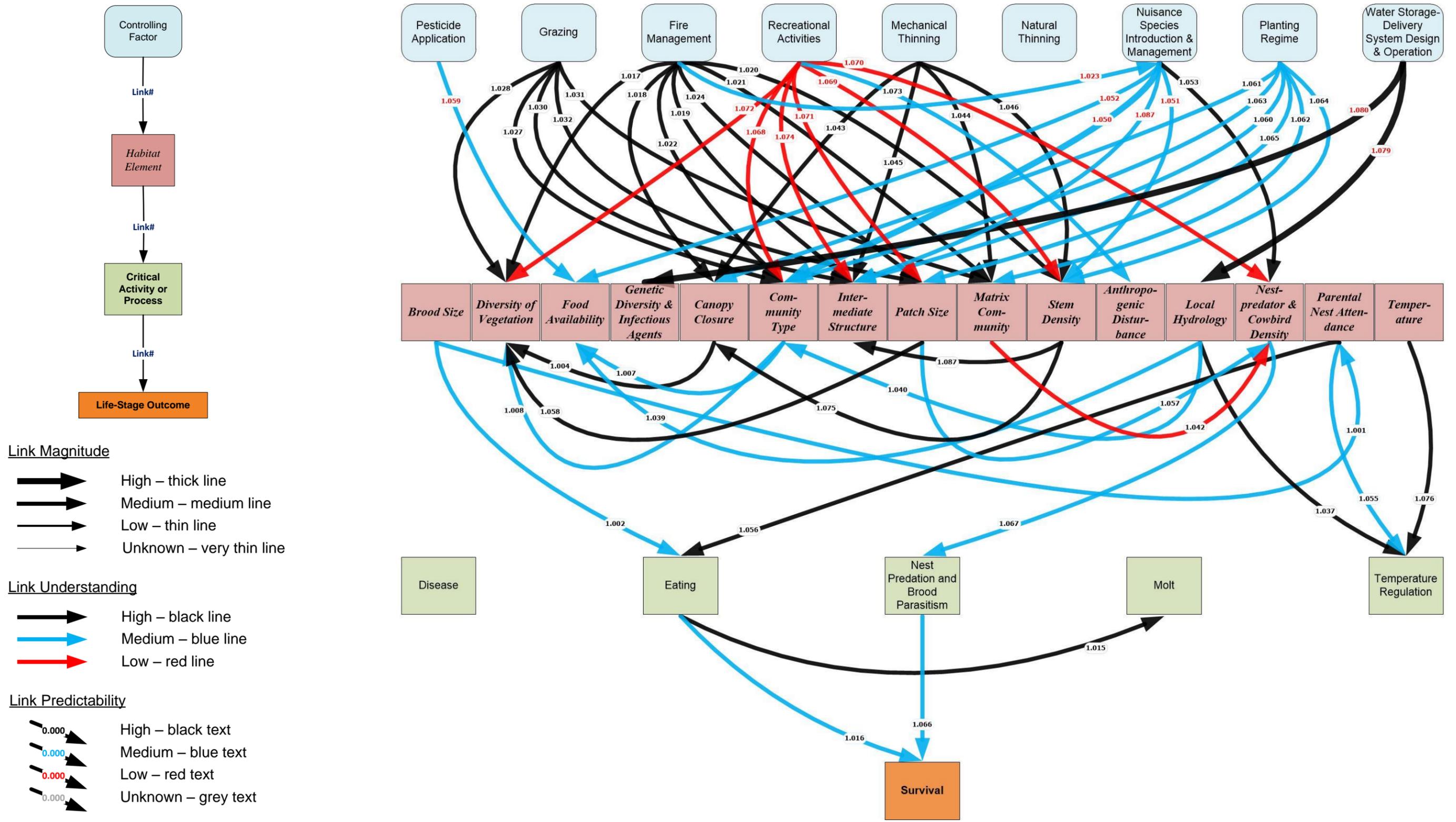


Figure 4.—BEVI life stage 1 – nest, high- and medium-magnitude relationships, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.

BEVI LIFE STAGE 2 – JUVENILE

The juvenile stage begins at fledging and ends when the bird returns to the breeding grounds the next year. However, for the sake of this analysis, we will only emphasize the period between fledging and migration.

Success during this life stage – successful transition to the next stage – involves organism survival and maturation. The organisms actively interact with their environment.

The CEM (figures 5 and 6) recognizes five (of nine) critical biological activities and processes for this life stage. Eating, nest attendance, nest predation and brood parasitism, and nest site selection are not included, as they are activities and processes of other life stages. The critical biological activities and processes are presented here, ordered as they appear on the following figures.

1. **Disease** – Although the literature does not emphasize disease as affecting population levels of BEVI, we still feel that disease bears mentioning. Diseases and parasites are prevalent in avian populations so it is safe to assume they have an impact on BEVI (Morishita et al. 1999; Lachish et al. 2011). Disease and parasite impacts along the LCR is recommended as an area of potential research.

The CEM recognizes genetic diversity and infectious agents as a habitat element affecting disease.

2. **Foraging** – Although still fed by its parents, the juvenile can now also forage for its own food in order to eat and maintain metabolic processes. The degree to which it is dependent upon foraging relates to the feeding rate of the parents and all of the factors affecting parental survival. Foraging directly affects survival.

The CEM recognizes anthropogenic disturbance, diversity of vegetation, food availability, the matrix community, and parental feeding behavior as habitat elements affecting foraging. In addition, disease can affect the foraging efficiency of a juvenile, but it is not known to what extent. Foraging, in turn, affects molt.

3. **Predation** – Predation directly affects survival.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, parental feeding behavior, predator density, and stem density as habitat elements directly affecting predation rates.

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4. **Molt** – Juvenile birds molt into adult-like plumage shortly after fledging.

No habitat elements directly influence molt, but many do indirectly through their impacts on foraging. Molt directly affects survival.

5. **Temperature Regulation** – The juvenile must maintain an optimum temperature to survive.

The CEM recognizes canopy closure, intermediate structure, local hydrology, and temperature as habitat elements directly affecting temperature regulation. The critical biological process and activity of disease can also influence temperature regulation.

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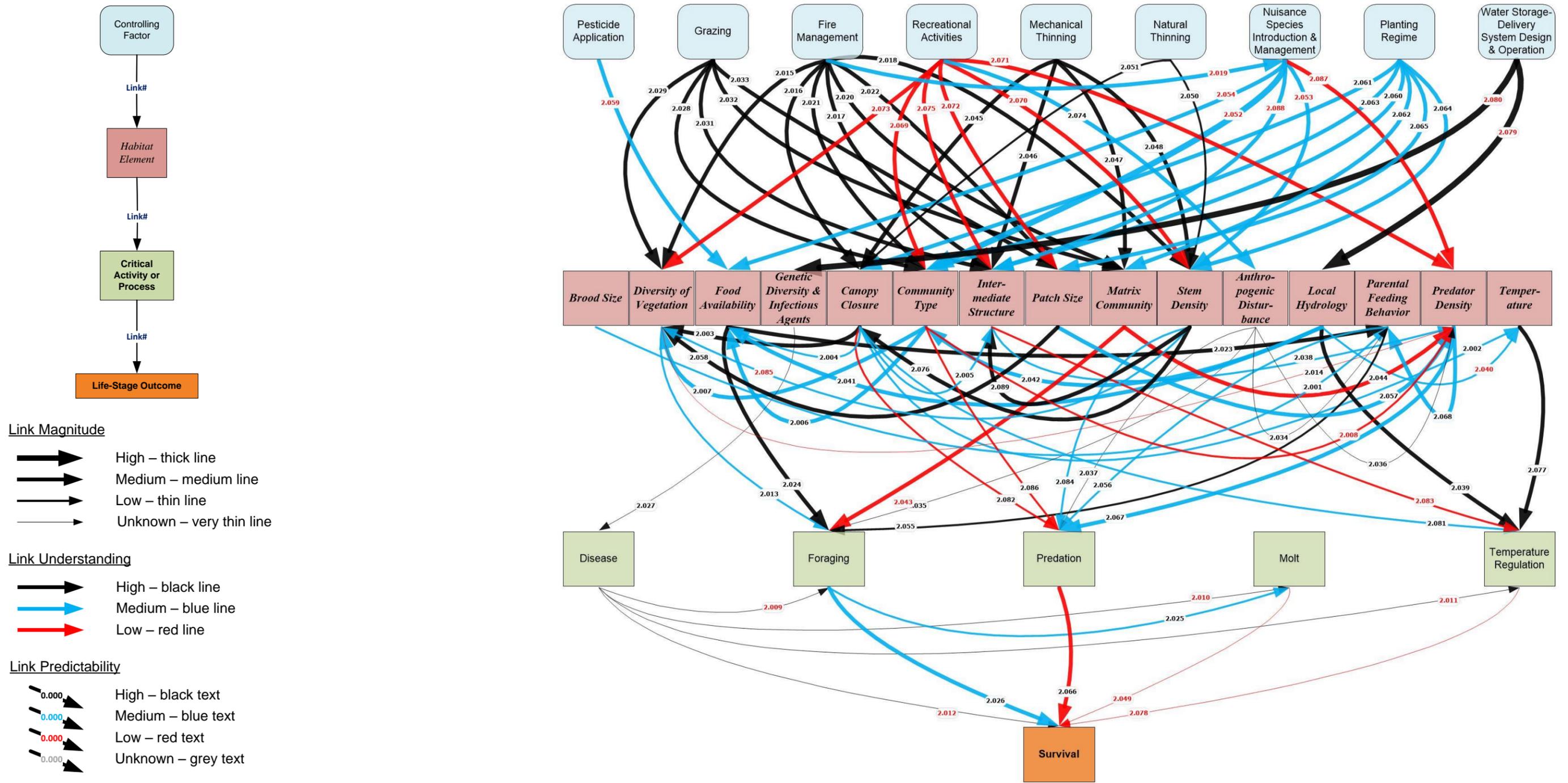


Figure 5.—BEVI life stage 2 – juvenile, basic CEM diagram, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.

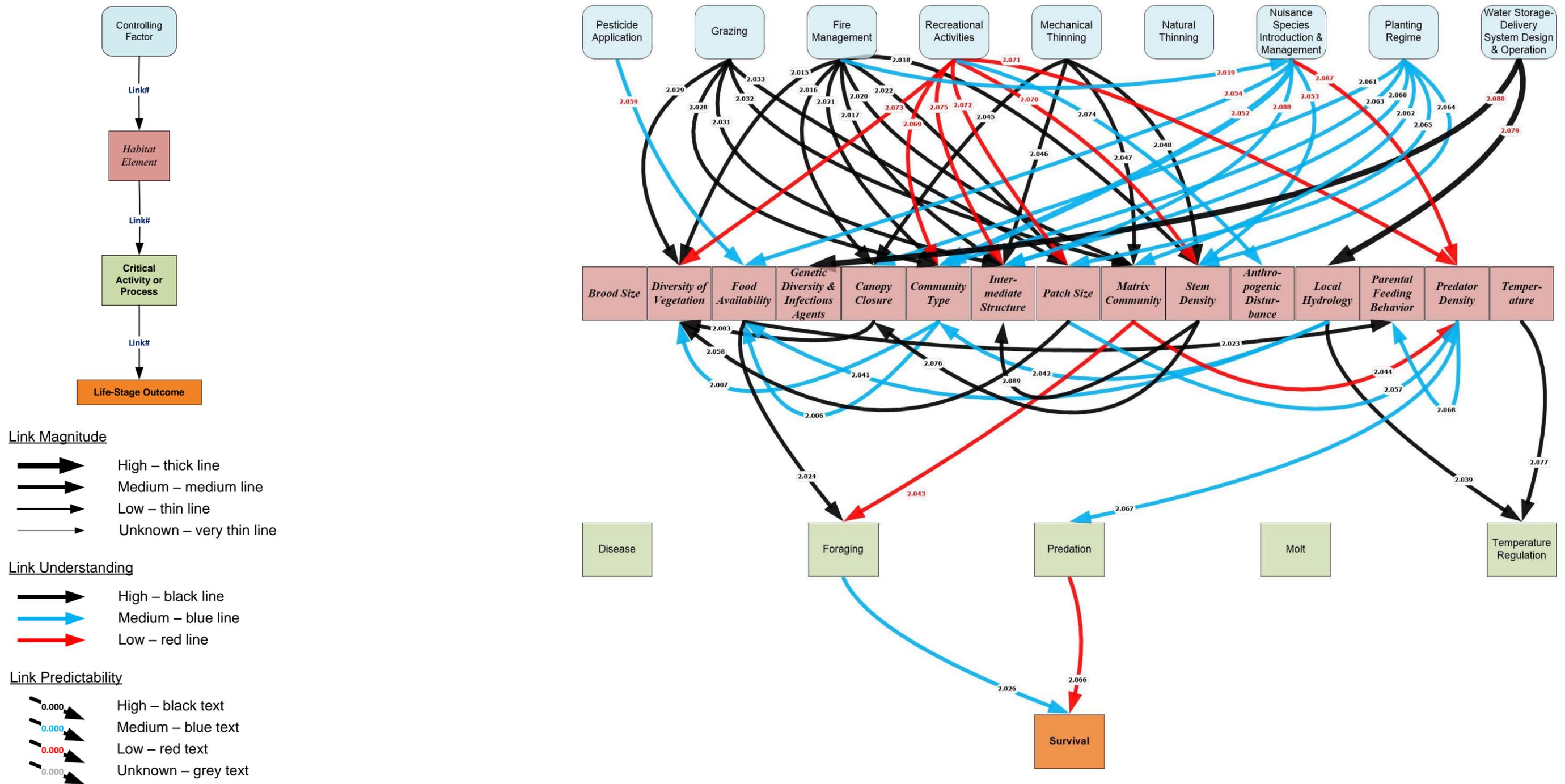


Figure 6.—BEVI life stage 2 – juvenile, high- and medium-magnitude relationships showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.

BEVI LIFE STAGE 3 – BREEDING ADULT

The breeding adult stage begins when the bird returns to the breeding grounds after its first or subsequent winter and ends when it departs the breeding grounds during fall migration. Success during this life stage – successful transition to the next stage – involves organism survival and breeding. Individuals that do not successfully find a territory, floaters, are also included in this category even though they do not breed. The organisms actively interact with their environment.

The CEM (figures 7 and 8) recognizes seven (of nine) critical biological activities and processes for this life stage. Eating and nest predation and brood parasitism are not included, as they are critical biological activities and processes of the nest life stage. The critical biological activities and processes are presented here, ordered as they appear on the following figures.

1. **Disease** – Although the literature does not emphasize disease as affecting population levels of BEVI, we still feel that disease bears mentioning. Diseases and parasites are prevalent in avian populations, so it is safe to assume they have an impact on BEVI (Morishita et al. 1999; Lachish et al. 2011). Disease and parasite impacts along the LCR is recommended as an area of potential research.

The CEM recognizes genetic diversity and infectious agents as a habitat element affecting disease.

2. **Foraging** – The breeding adult must forage to feed itself and its young. Survival of adults and their young are dependent upon the foraging rate, which can be influenced by a number of factors.

The CEM recognizes anthropogenic disturbance, brood size, diversity of vegetation, food availability, and the matrix community as habitat elements affecting foraging. Foraging is affected by the critical biological activities and processes of disease and directly affects molt, nest attendance, and survival.

3. **Predation** – Adults must avoid predation to survive.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, predator density, and stem density as the primary habitat elements affecting predation.

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4. **Nest Attendance** – The breeding adult must attend the nest to incubate eggs, brood young, and feed young, thus directly affecting reproductive output.

The CEM recognizes anthropogenic disturbance, brood size, food availability, local hydrology, predator density, and temperature as the top habitat elements affecting nest attendance. Nest attendance is affected by the critical biological activities and processes of disease and foraging.

5. **Nest Site Selection** – This process includes both territory establishment and the selection of the actual nest site. Territory establishment is especially important because if a bird fails to establish a territory (or find a male with a territory in the case of females), the bird will be a floater and is unlikely to breed during that season. The breeding adult must choose where to place territories and construct nests, thereby affecting breeding success (reproductive output).

The CEM recognizes anthropogenic disturbance, canopy closure, community type, diversity of vegetation, food availability, intermediate structure, local hydrology, patch size, predator density, previous year's use, stem density, and temperature as the primary habitat elements affecting nest site selection.

6. **Molt** – Breeding adults undergo a post-nuptial molt each year. This activity takes resources, which must be directed from other biological processes. Molt requires food (through foraging) and is impacted by disease. The result is that other aspects of survival may be affected, but flight capability should improve.

The CEM does not recognize any habitat variables that directly influence molt.

7. **Temperature Regulation** – The adult must maintain an optimum temperature to survive.

The CEM recognizes canopy closure, intermediate structure, local hydrology, and temperature as the top habitat elements affecting temperature regulation, with nest site selection and disease as the critical biological activities and processes that directly affect temperature regulation.

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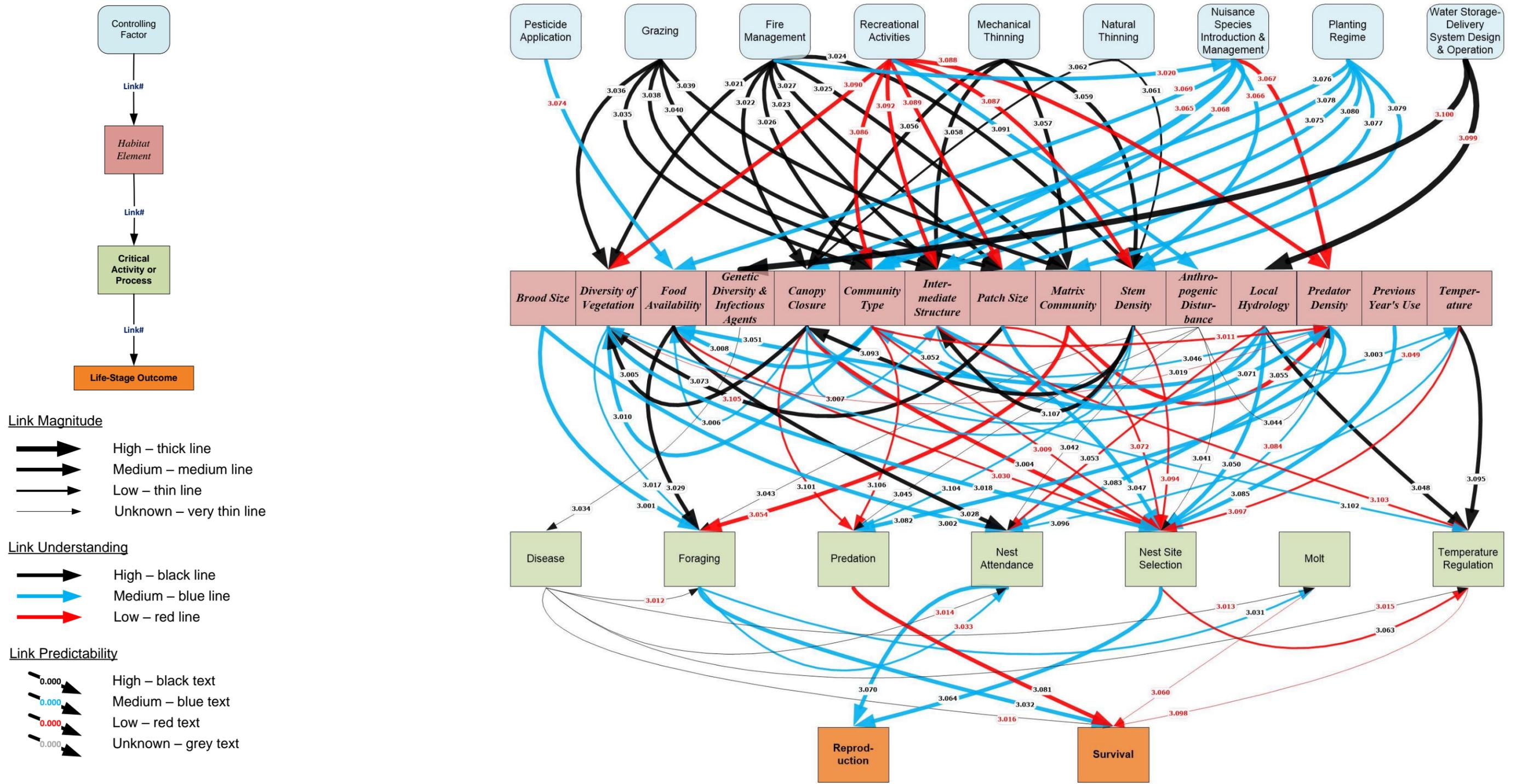


Figure 7.—BEVI life stage 3 – breeding adult, basic CEM diagram, showing the relevant controlling factors, habitat elements, and critical biological activities and processes at this life stage.

Chapter 7 – Causal Relationships Across All Life Stages

The nine controlling factors discussed in chapter 5 have the same influence on the same habitat elements for all life stages for which those habitat elements matter. Table 5 shows the magnitudes of *direct* influence of the 9 controlling factors on the 18 habitat elements. The structure of table 5 is the same as for table 4, but table 5 shows the magnitudes of the relationships instead of just their presence/absence. The paragraphs following the table discuss the relative effects of the different controlling factors on each habitat element. The magnitudes of direct influences of controlling factors on habitat elements is color coded in the table as follows:

High = H, Medium = M, and Low = L

Table 5.—Magnitude of influence of controlling factors on habitat elements

Controlling factor →									
Habitat element ↓	Fire management	Grazing	Mechanical thinning	Natural thinning	Nuisance species introduction and management	Pesticide/herbicide application	Planting regime	Recreational activities	Water storage-delivery system design and operation
Anthropogenic disturbance								M	
Brood size	N/A*								
Canopy closure	M		M	M			M		
Community type	M	M			H		M	M	
Diversity of vegetation	M	M						M	
Food availability					M	L	M		
Genetic diversity and infectious agents									H
Intermediate structure	M	M	M		M		M	M	H
Local hydrology									H
Matrix community	M	M	M				M		
Nest predator and cowbird density					M			M	
Parental feeding behavior	N/A*								
Parental nest attendance	N/A*								
Patch size	M	M					M	M	
Predator density					M			M	
Previous year's use	N/A*								
Stem density	M	M	M	M	M		M	M	
Temperature	N/A*								

* N/A values suggest that none of the identified controlling factors *directly* affect the habitat element.

ANTHROPOGENIC DISTURBANCE

Recreational activities are the main controlling factor that affect anthropogenic disturbance. All activities involving humans increase anthropogenic noise, a major component of anthropogenic disturbance. The scale and scope of the influences depend upon the scale and scope of the activity. In general, most activities are of narrow scope and short duration; however, systematic influences can cause repeated noise or other disturbances (e.g., campsites, ORV trails, or nearby roads).

CANOPY CLOSURE

The controlling factors that directly affect canopy closure include fire management, mechanical thinning, natural thinning, and planting regime. Natural and mechanical thinning will reduce canopy closure; however, the effects of fire management and planting regime depend on the management actions and species involved.

Fire affects many aspects of vegetation structure and composition and can destroy riparian habitat. Fire management can have great effects on vegetation structure and is usually implemented over large areas. However, the dynamic nature of both fire and riparian communities means that the effects of fire management will likely last less than a decade.

Mechanical thinning is generally performed at the patch level, with effects lasting until vegetation grows back, and can be as intense as managers wish.

Although natural thinning affects canopy closure, it works on small scales, creating forest gaps. The effect only lasts until the vegetation grows back.

Planting regimes have the ability to greatly affect vegetation. However, planting decisions are made at the scale of an individual restoration site. Although riparian communities tend to be ephemeral, restoration sites are heavily managed, so the effects are likely medium or even long term.

COMMUNITY TYPE

The controlling factors that directly affect community type are fire management, grazing, nuisance species introduction and management, planting regime, and recreational activities. It is not possible to state whether the effects of controlling factors are positive or negative, as community type is not a numeric variable.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
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Fire affects many aspects of vegetation structure and composition and can destroy habitat (Engstrom et al. 1984). Fire management can have great effects on vegetation structure, and thus community type, and is usually implemented over either small or large areas. However, the dynamic nature of both fire and riparian communities means that effects of fire management will likely last less than a decade.

Grazing affects many aspects of riparian vegetation structure and composition (Kauffman et al. 1997). Grazing activity can have great effects on community composition and is often implemented over large and long scales (Kauffman et al. 1997). However, the dynamic nature of riparian communities means that effects of grazing will likely last less than a decade unless a complete transformation of the community type occurs.

Nuisance species can change the structure of entire communities with lasting effects. However, although the effects are experienced at a patch level, nuisance invasive species can spread across entire regions, and their effects can last decades if not cause a permanent transition to a new community type.

Planting regimes have the ability to greatly affect vegetation. However, planting decisions are made at the scale of individual restoration sites. Although riparian communities tend to be ephemeral, restoration sites are heavily managed, so the effects are likely medium or even long term.

Recreational activities can influence the species composition of a riparian forest, although it depends on the activity.

DIVERSITY OF VEGETATION

The controlling factors that directly affect diversity of vegetation are fire management, grazing, and recreational activities. It is not possible to state whether the effects of controlling factors are positive or negative, as vegetation diversity is not a numeric variable.

Fire affects many aspects of vegetation structure and composition and can destroy habitat (Engstrom et al. 1984). Fire management can have great effects on vegetation structure and diversity and is usually implemented over either small or large areas. However, the dynamic nature of both fire and riparian communities means that effects of fire management will likely last less than a decade.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

Grazing affects many aspects of riparian vegetation structure and composition (Kauffman et al. 1997). Grazing activity can have great effects on community composition and is often implemented over large and long scales (Kauffman et al. 1997). However, the dynamic nature of riparian communities means that effects of grazing will likely last less than a decade unless a complete transformation of the community type occurs.

Recreational activities can alter vegetation diversity, although the effects depend on the type, duration, and scope of the particular activity.

FOOD AVAILABILITY

The controlling factors that directly affect the food available to a BEVI include nuisance species introduction and management, pesticide/herbicide application, and planting regime.

Nuisance species can change an arthropod community; however, other factors also affect arthropod availability. The effects of nuisance invasive species can spread across entire regions and last for decades.

The magnitude of the effect of pesticide/herbicide use depends on many factors, but the potential magnitude is very high. However, the most likely scenario involves pesticide/herbicide applications at individual agricultural fields affecting nearby patches and the effects dissipating less than a decade after application.

Planting regimes have the ability to greatly affect vegetation, which in turn, affect the invertebrate species composition of a patch in any given year. However, planting decisions are made at the scale of individual restoration sites.

GENETIC DIVERSITY AND INFECTIOUS AGENTS

Water storage-delivery system design and operation can affect genetic diversity in part by fragmenting riparian habitat used by BEVI. Effects of population isolation can be long term.

INTERMEDIATE STRUCTURE

The controlling factors that directly affect intermediate structure include fire management, grazing, mechanical thinning, nuisance species introduction and management, planting regime, and recreational activities. Fire, grazing,

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Basic Conceptual Ecological Model for the Lower Colorado River**

recreational activities, and mechanical thinning will generally reduce intermediate structure, whereas the effects of nuisance species introduction and management and the planting regime depend on the management actions and species involved.

Fire affects many aspects of vegetation structure and composition and can destroy BEVI habitat. Fire management can have great effects on vegetation structure and is usually implemented over large areas.

Grazing affects many aspects of riparian vegetation structure and composition (Kauffman et al. 1997). Grazing activity can have great effects on community composition and is often implemented over large and long scales (Kauffman et al. 1997). However, the dynamic nature of riparian communities means that the effects of grazing will likely last less than a decade but only if grazing is removed and a permanent transition of the habitat has not occurred.

Mechanical thinning is generally performed at the patch level, with effects lasting until vegetation grows back, and can be as intense as managers deem necessary.

Nuisance species can change the structure of entire communities, with lasting effects. Although the effects are experienced at a patch level, nuisance invasive species can spread across entire regions, and their effects can last decades.

Planting regimes have the ability to greatly affect vegetation. However, planting decisions are made at the scale of individual restoration sites.

Finally, the potential impact of recreational activities on BEVI habitat is great, although it depends on the activity. Decisions regarding management of recreational activities can affect large areas.

LOCAL HYDROLOGY

One controlling factor influences local hydrology: water storage-delivery system design and operation. It is not possible to put a direction on the effect. The amount of water released or stored by dams affects water levels and therefore distance to water, soil moisture, humidity, and other related hydrological conditions. Water storage and flow regimes can affect vegetation communities and food abundance (Nilsson and Svedmark 2002; Burke et al. 2009) via local hydrology. The effects of water storage-delivery system design and operation spreads over large scales, but the effects of changes in flow regimes likely last less than a decade unless a complete transformation of the habitat occurs.

MATRIX COMMUNITY

The controlling factors that directly affect the matrix community include fire management, grazing, mechanical thinning, and the planting regime. However, it is difficult to predict effects given the variety of management options and the fact that BEVI use of a matrix community is at the landscape level.

Fire affects many aspects of vegetation structure and composition and can destroy BEVI habitat. Fire management can have great effects on vegetation structure and is usually implemented over large areas.

Grazing affects many aspects of riparian vegetation structure and composition (Kauffman et al. 1997). Grazing activity can have great effects on community composition and is often implemented over large and long scales (Kauffman et al. 1997). However, the dynamic nature of riparian communities means that effects of grazing will likely last less than a decade, but only if grazing is removed and a permanent transition of the habitat has not occurred.

Mechanical thinning is generally performed at the patch level, with effects lasting until vegetation grows back, and can be as intense as managers deem necessary.

The effects of any planting regime depend on the management actions and species involved.

NEST PREDATOR AND COWBIRD DENSITY

The controlling factors directly affecting nest predator and cowbird density include nuisance species introduction and management and recreational activities. The direction and size of these effects are difficult to quantify.

Nuisance species control efforts (or lack of them) can affect the densities of cowbirds, affecting BEVI nest success.

Recreational activities can influence nest predator densities by either increasing predator success rates through interfering with or distracting prey or by decreasing predator success rates through interfering with or distracting the predator (Mason 2015; Ware et al. 2015).

PATCH SIZE

The controlling factors that directly affect patch size include fire management, grazing, planting regime, and recreational activities. Fire management, grazing,

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

and recreational activities will generally reduce the size of a given patch, whereas the effects of planting regime depend on the management actions and species involved.

Fire affects many aspects of vegetation structure and composition and can destroy habitat (Engstrom et al. 1984). Fire management can have great effects on vegetation structure, and thus patch size, and can be implemented over either small or large areas. However, the dynamic nature of both fire and riparian communities means that the effects of fire management will likely be short term.

Grazing affects many aspects of riparian vegetation structure and composition (Kauffman et al. 1997). Grazing activity can have great effects on community composition and patch size and is often implemented over large and long scales (Kauffman et al. 1997). However, the dynamic nature of riparian communities means that the effects of grazing will likely be short term in nature unless a permanent transition in the patch occurs.

Planting regimes have the ability to greatly affect vegetation. However, planting decisions are made at the scale of individual restoration sites. Although riparian communities tend to be ephemeral, restoration sites are heavily managed, so the effects are likely medium or even long term, and patch size can be integrated into restoration planning.

Recreational activities can influence the species composition of a riparian forest, although it depends on the activity.

PREDATOR DENSITY

The controlling factors directly affecting predator density include nuisance species introduction and management and recreational activities. The direction and size of these effects are difficult to quantify.

Nuisance species introduction and management can change the community, and some studies have shown that predator presence differs among community types, particularly between native and non-native habitats (Schmidt et al. 2005). Although the effects are experienced at a patch level, nuisance invasive species can spread across entire regions, and their effects can last decades.

Recreational activities can influence predator density by either increasing predator success rates through interfering with or distracting prey or by decreasing predator success rates through interfering with or distracting the predator (Mason 2015; Ware et al. 2015).

STEM DENSITY

The controlling factors that directly affect stem density include fire management, grazing, mechanical thinning, natural thinning, nuisance species introduction and management, planting regime, and recreational activities. Fire, mechanical thinning, and recreational activities will generally reduce tree and/or shrub density, whereas the effects of nuisance species introduction and management and the planting regime depend on the management actions and species involved.

Fire affects many aspects of vegetation structure and composition and can destroy BEVI habitat (Engstrom et al. 1984). Fire management can have great effects on vegetation structure and is usually implemented over large areas. However, the dynamic nature of both fire and riparian communities means that effects of fire management will likely last less than a decade.

Mechanical thinning is generally performed at the patch level, with effects lasting until vegetation grows back, and can be as intense as managers deem necessary.

Although natural thinning affects canopy closure, it works on small scales, creating forest gaps. The effect only lasts until the vegetation grows back.

Nuisance species can change the structure of entire communities, with lasting effects. Although the effects are experienced at a patch level, nuisance invasive species can spread across entire regions, and their effects can last decades if not resulting in a permanent transformation.

Planting regimes have the ability to greatly affect vegetation. However, planting decisions are made at the scale of an individual restoration site. Although riparian communities tend to be ephemeral, restoration sites are heavily managed, so the effects are likely medium or even long term.

Finally, the potential impact of recreation on BEVI habitat is great, although it depends on the activity. Decisions regarding management of recreational activities can affect large areas.

Chapter 8 – Discussion and Conclusions

This chapter summarizes the findings of the assessment in three ways by posing three questions: (1) which critical biological activities and processes most strongly affect the individual life stages across all life stages, (2) which habitat elements, in terms of their abundance, distribution, and quality, most strongly affect the most influential activities and processes, and (3) which of these causal relationships appear to be the least understood in ways that could affect their management?

MOST INFLUENTIAL ACTIVITIES AND PROCESSES ACROSS ALL LIFE STAGE

Figure 9 identifies the critical biological activities and processes that the assessment found most strongly directly affect the success of each life stage (high or medium magnitude). The findings presented in this diagram may be summarized as follows:

- Predation (nest predation and brood parasitism in the nest stage) and foraging (eating in nest stage) are the most important critical biological activities and processes affecting survival of BEVI at all life stages. Other processes such as disease, molt, and temperature regulation can be very important, but are less understood, especially within the LCR.
- Only two processes directly affect reproduction—nest attendance and nest site selection. Nest site selection is especially important, as it can indirectly influence survival of BEVI at all life stages. For example, good nest sites may have more food, fewer predators, and fewer diseases present.

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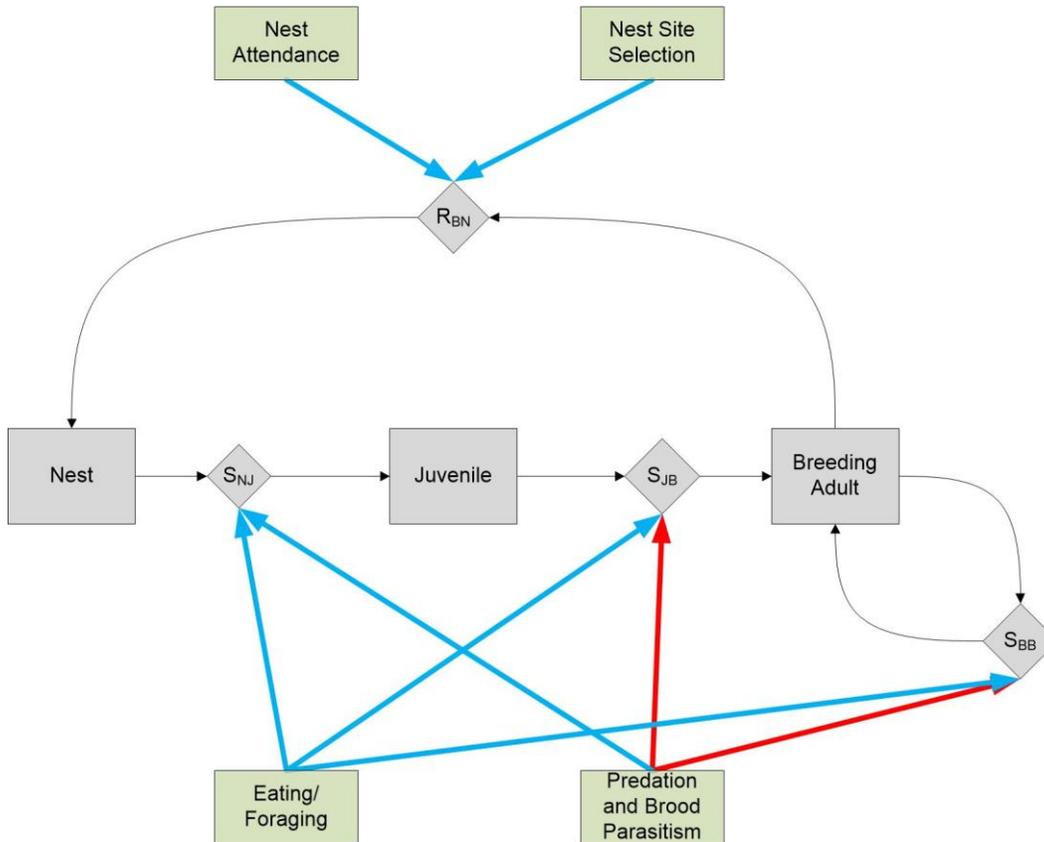


Figure 9.—Most influential biological activities and processes affecting each life stage of BEVI. Only elements with high- or medium-magnitude connections are presented. The legend is provided on figure 2.

POTENTIALLY PIVOTAL ALTERATIONS TO HABITAT ELEMENTS

Figure 10 identifies the habitat elements that this assessment indicates most strongly directly affect the critical biological activities and processes identified on figure 9 across all life stages (high or medium magnitude). The findings presented in this diagram may be summarized as follows:

- Nest site selection is by far affected by the most habitat variables likely because this critical biological activity is not only the most researched element but also because during the breeding season, nest site selection determines whether birds are present or not.

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
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- A number of factors directly influence a juvenile or adult individual's ability to acquire sufficient food – most strongly are brood size, food availability, and the matrix community, as BEVI may forage there. Although less intense, other habitat elements such as anthropogenic disturbance, diversity of vegetation, local hydrology, and temperature also directly or indirectly affect foraging.
- Nest predation/predation is influenced directly and strongly by the density of predators and/or brood parasites at a site. Other habitat elements, such as community type and patch size, may determine, in part, which predators are present and more or less successful. Predator density affects predation rates (Lima 2009).
- Nest attendance is strongly affected by brood size, food availability, and predator density. Anthropogenic disturbance, local hydrology, and temperature influence nest attendance either directly or by strong indirect effects on other habitat elements.
- Disease and temperature regulation are important physiological concerns impacted most strongly by habitat elements such as genetic diversity and infectious agents, local hydrology (as it affects humidity), and temperature. However, the strengths and effects of these interactions remain unknown.

GAPS IN UNDERSTANDING

Figures 9 and 10 use the conventional color coding of individual causal relationships to identify relationships that the CEM identifies as having high, intermediate, or low levels of scientific confirmation. As noted in attachment 1, “Low” scientific understanding of a relationship means that it is “... subject to wide disagreement or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.” In many cases, the scientific principles are well understood, but the factual details are insufficiently understood within the LCR. The two figures show some red arrows, indicating relationships that the assessment identifies as having a low level of scientific understanding. Each of these red arrows identifies a causal relationship that may warrant further field, laboratory, or literature investigation. The following paragraphs highlight some potentially important areas of low understanding:

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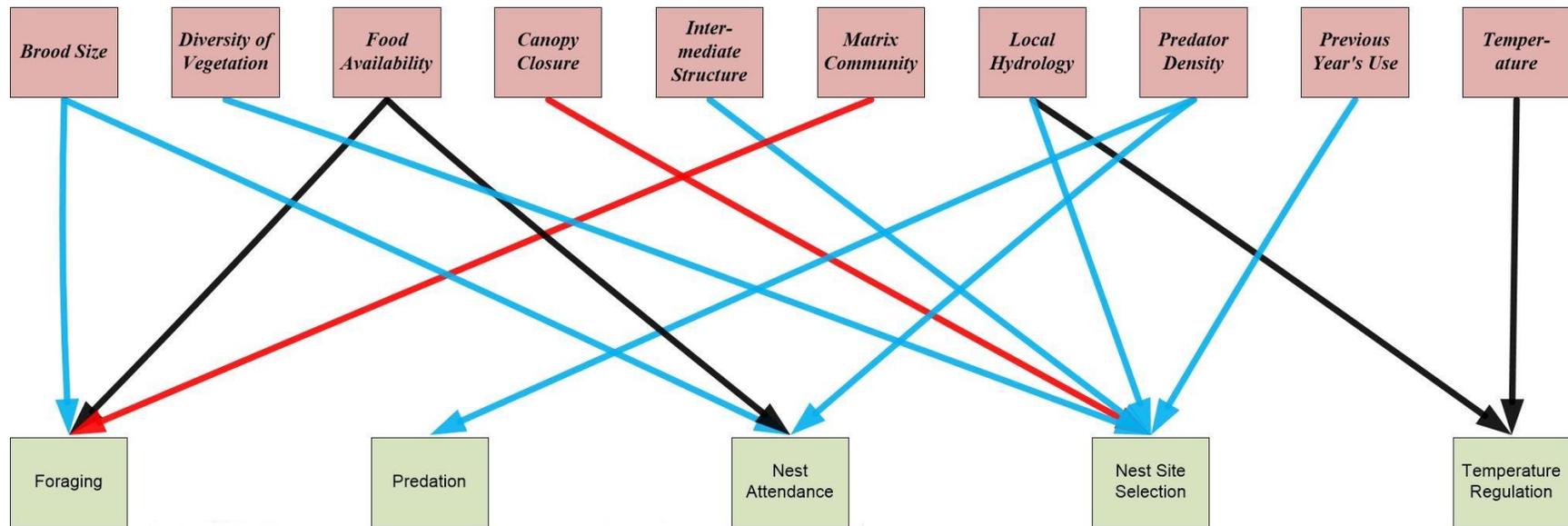


Figure 10.—Habitat elements that directly or indirectly affect the most influential biological activities and processes across all life stages of BEVI. Only elements with high- or medium-magnitude connections within this life stage are presented. The legend is provided on figure 2.

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Basic Conceptual Ecological Model for the Lower Colorado River**

- Nest site selection is potentially affected by the most habitat variables, and much data have been collected along the LCR for BEVI (A. Leist 2015, personal communication). Pending data analyses will help clarify which habitat parameters (e.g., humidity at the nest, intermediate structure, patch size and other patch characteristics, etc.) are driving nest site selection in the LCR for this species. The effects of anthropogenic disturbance and predator density on nest attendance and nest site selection remain poorly understood for all bird species, and have not been studied in BEVI.
- The effects of disease, ecto-parasites, and endo-parasites have not been studied in BEVI or among passerine species inhabiting the LCR. Diseases have the potential to have dramatic impacts on populations (Robinson et al. 2010).
- What is the current level of cowbird parasitism of BEVI along the LCR? Are there other actions that need to be taken to improve nest success?
- BEVI exhibit site fidelity. Does this contribute to greater nest success?
- How important is canopy closure to BEVI in nest site selection, foraging, or other activities?
- What are the effects of anthropogenic disturbance on BEVI nest site selection and behavior, and what influences do different types of disturbances have on nesting success?
- How will climate change affect BEVI habitat vegetation phenology, nest site selection, and nest success? What management actions can be used to address this?
- Klicka et al. (2015) describe the first genetic analysis of the Bell's vireo across all its range in North America and recommend that the Bell's vireo should be divided into two species on an east/west divide, with the western species being named the least vireo (*Vireo pusillus*). They also support the idea of two subspecies for the western population. Additional genetic studies are needed to resolve the taxonomic status of the western subspecies (BEVI and least bell's vireo) and better assess their distributions. This may also help clarify the potential for recolonization across the LCR in suitable habitats.
- How much do BEVI rely on matrix communities for foraging? What other influences do matrix communities and land management on these surrounding lands have on BEVI habitat use and reproductive success?

**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
Basic Conceptual Ecological Model for the Lower Colorado River**

This list of uncertainties is not meant to be exhaustive but only to highlight topics the literature identifies as potentially pivotal to BEVI recruitment along the LCR and to identify important knowledge gaps in these publications. They are not in any way to be considered guidance for Reclamation or the LCR MSCP, nor are these knowledge gaps expected to be addressed under the program. Fortunately, some of the data that can address these questions and guide future management have already been gathered and are awaiting analyses (A. Leist 2015, personal communication).

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**Arizona Bell's Vireo (*Vireo bellii arizonae*) (BEVI)
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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 (Wildhaber et al. 2007; Fischenich 2008; DiGennaro et al. 2012). 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 Wildhaber et al. (2007), Kondolf et al. (2008), Burke et al. (2009), and Wildhaber (2011) for a more hierarchical approach and adds explicit demographic notation for the characterization of life-stage outcomes (McDonald and Caswell 1993). This expanded approach provides greater detail on causal linkages and outcomes. The expansion specifically calls for identifying **four** types of model components for each life stage, and the causal linkages among them, as follows:

- **Life-stage outcomes** are outcomes of an individual life stage, including the recruitment of individuals to the next succeeding life stage (e.g., juvenile to adult). For some life stages, the outcomes, alternatively or additionally, may include the survival of individuals to an older age class within the same life stage or the production of offspring. The rates of life-stage outcomes depend on the rates of the critical biological activities and processes for that life stage.
- **Critical biological activities and processes** are activities in which a species engages and the biological processes that must take place during each life stage that significantly affect life-stage outcomes. They include activities and processes that may benefit or degrade life-stage outcomes. Examples of critical activities and processes include mating, foraging, avoiding predators, avoiding other specific hazards, gamete production, egg maturation, leaf production, and seed germination. Critical activities and processes are “rate” variables. Taken together, the rate (intensity) of these activities and processes determine the rates of different life-stage outcomes.
- **Habitat elements** are specific habitat conditions that significantly ensure, allow, or interfere with critical biological activities and processes. The full suite of natural habitat elements constitutes the natural habitat template for a given life stage. Human activities may introduce habitat elements not present in the natural habitat template. Defining a habitat element may involve estimating the specific ranges of quantifiable properties of that element *whenever the state of knowledge supports such estimates*. These properties concern the abundance, spatial and temporal distributions, and other qualities of the habitat element that significantly affect the ways in which it ensures, allows, or interferes with critical biological activities and processes.
- **Controlling factors** are environmental conditions and dynamics – both natural and anthropogenic – that determine the quality, abundance, and spatial and temporal distributions of one or more habitat elements. In some instances, a controlling factor alternatively or additionally may directly affect a critical biological activity or process. Controlling factors are also called “drivers.” A hierarchy of controlling factors will exist, affecting the system at different temporal and spatial scales. Long-term dynamics of climate and geology define the domain of this hierarchy (Burke et al. 2009). For example, the availability of suitable nest sites for a riparian nesting bird may depend on factors such as canopy closure, community type, humidity, and intermediate structure which, in turn, may depend on factors such as water storage-delivery system design and operation (dam design, reservoir morphology, and dam operations) which, in turn, is shaped by watershed geology, vegetation, climate, land use, and water demand. *The LCR MSCP conceptual ecological models focus*

on controlling factors that are within the scope of potential human manipulation, including management actions directed toward the species of interest.

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

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

- (1) The effect of one controlling factor on another
- (2) The effect of a controlling factor on the abundance, spatial and temporal distributions, and other qualities of a habitat element
- (3) The effect of the abundance, spatial and temporal distributions, and other qualities of one habitat element on those of another
- (4) The effect of the abundance, spatial and temporal distributions, and other qualities of a habitat element on a critical biological activity or process
- (5) The effect of one critical biological activity or process on another
- (6) The effect of a critical biological activity or process on a specific life-stage outcome

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

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

Conceptual Ecological Models as Hypotheses

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

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

Characterizing Causal Relationships

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

- (1) The character and direction of the effect
- (2) The magnitude of the effect
- (3) The predictability (consistency) of the effect
- (4) The certainty of present scientific understanding of the effect

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

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

Third, the ERP methodology addresses a single, large landscape, while the present methodology needed the flexibility to generate models applicable to a variety of spatial scopes. For example, the present methodology needed to support modeling of a single restoration site, the LCR main stem and flood plain, 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 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.

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

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

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

Link Attribute Ratings, Spreadsheet Fields, and Diagram Conventions

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

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

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

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

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

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 <i>management actions and options</i> , with reasoning, including the estimate of relative importance when possible.
W	Research Questions	Brief notes that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in <i>basic scientific knowledge</i> , with reasoning, including the estimate of relative importance when possible.
X	Other Comments	Provides additional notes on investigator concerns, uncertainties, and questions.
Y	Update Status	Provides information on the history of editing the information on this link for updates carried out after completion of an initial version.

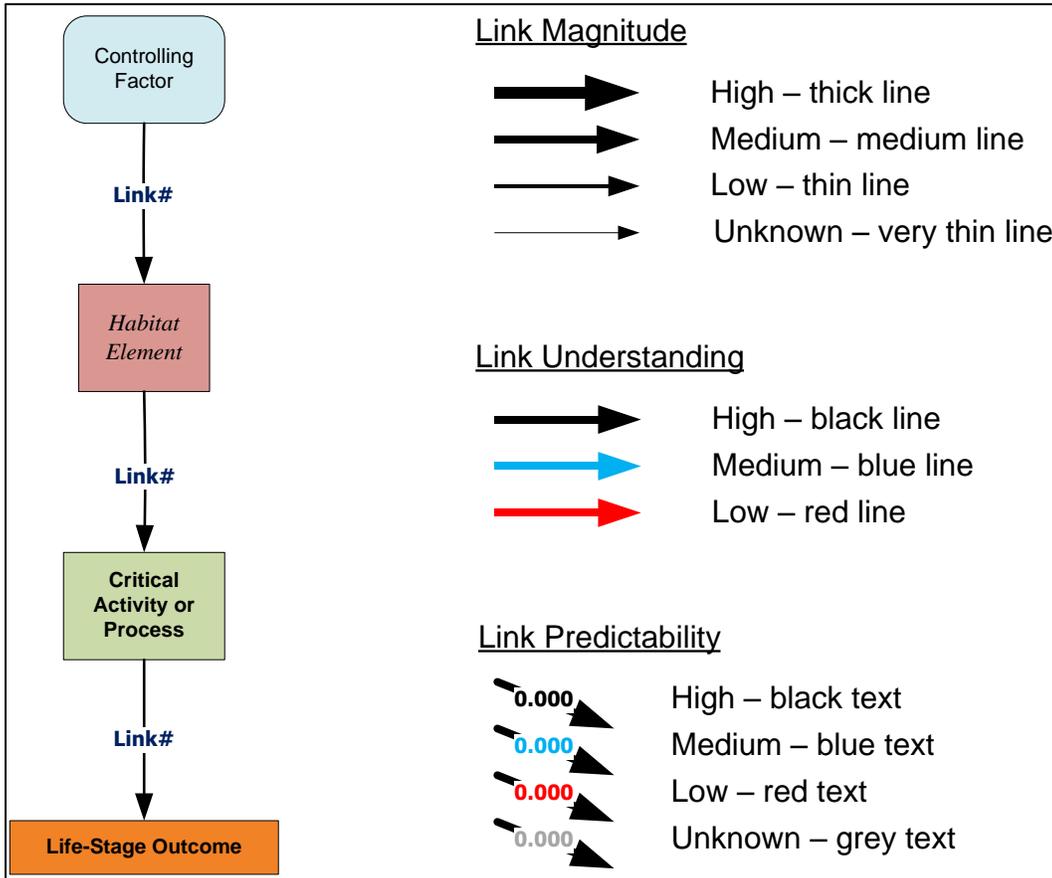


Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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ATTACHMENT 2

Arizona Bell's Vireo Habitat Data

Table 2-1.—Arizona Bell's vireo (BEVI) habitat data

Habitat element	Value or range	Location	Reference
Anthropogenic disturbance	Anthropogenic disturbance caused premature fledging.	Kansas	Barlow 1962
	Effects of disturbance, including noise, not quantified in lower Colorado River.		
Canopy closure	BEVI select sites with more patchy or open canopy than other riparian birds; overstory open or absent.	Various	Kus et al. 2010
	BEVI nests in sites with significantly greater canopy closure than non-use sites.	Lower Colorado River	Great Basin Bird Observatory (GBBO) 2011
Community type	Mature cottonwood-willow (<i>Populus fremontii</i> , <i>Salix</i> sp.), mesquite (<i>Prosopis</i> sp.), seep willow (<i>Baccharis salicifolia</i>), salt cedar (<i>Tamarix</i> sp.), arrowweed (<i>Pluchea sericea</i>).	Southwestern United States	Grinnell 1914; Bent 1950; Kus et al. 2010
	BEVI territories have significantly less upland habitat than non-use sites.	Lower Colorado River	GBBO 2011
	Will nest in salt cedar.	Lower Colorado River	Averill-Murray et al. 1999
Diversity of vegetation	BEVI prefer dense cover near openings in which they can forage.	Bill Williams River National Wildlife Refuge, Arizona	GBBO 2011
	Nest near edge of thicket; usually edges without overstory.	Various	Kus et al. 2010
Food availability	Taxa include: Hemiptera, Coleoptera, Lepidopteran larvae, Orthoptera, Diptera, and Aranea (spiders).	Lower Colorado River	Yard et al. 2004
Genetic diversity and infectious agents	No data available.		
Local hydrology	Standing water within 1,000 meters (0.6 mile)	California	Kus et al. 2010

Table 2-1.—Arizona Bell's vireo (BEVI) habitat data

Habitat element	Value or range	Location	Reference
Matrix community	Optimal matrix community is natural habitat (e.g., wetlands, better than golf course); a surrounding matrix of agricultural or urban land reduced nest success.	California	Kus et al. 2008
Nest predator and cowbird density	Cowbird densities < 30 percent needed to maintain populations.	California	Laymon 1987
Patch size	Least bell's vireo – larger cottonwood-willow patches best, 160 hectares (ha)	California	Lynn 1996, Kus et al. 2010
	Average territory size for least bell's vireo – 1.8 acres (0.7 ha)	California	Kus et al. 2010
	Linear territory 200 yards long.	California	Grinnell 1914
Predator density	There are no data related to predator density and BEVI survival or breeding success. Only species lists available.		
Previous year's use	Bell's vireos return to the same nesting territory year after year.	California	Greaves 1989; Franzreb 1989 <i>in</i> Kus et al. 2010
	Juveniles return to natal area to breed.	California	Greaves and Gray 1991
Stem density	Data awaiting analysis.		Leist 2015, personal communication
Temperature	BEVI change temperature regulatory behavior between 29 and 31 degrees Celsius (84–88 degrees Fahrenheit)	Lower Colorado River	Theimer et al. 2011
Intermediate structure	Dense vegetation within 1–3 meters of ground.	California	Goldwasser 1981; Franzreb 1989 <i>in</i> Kus et al. 2010
	No published densiometer data available.	Lower Colorado River	Leist 2015, personal communication

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