



Lower Colorado River Multi-Species Conservation Program

Balancing Resource Use and Conservation

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL) Basic Conceptual Ecological Model for the Lower Colorado River



Photo courtesy of the Bureau of Reclamation



September 2016

Lower Colorado River Multi-Species Conservation Program Steering Committee Members

Federal Participant Group

Bureau of Reclamation
U.S. Fish and Wildlife Service
National Park Service
Bureau of Land Management
Bureau of Indian Affairs
Western Area Power Administration

Arizona Participant Group

Arizona Department of Water Resources
Arizona Electric Power Cooperative, Inc.
Arizona Game and Fish Department
Arizona Power Authority
Central Arizona Water Conservation District
Cibola Valley Irrigation and Drainage District
City of Bullhead City
City of Lake Havasu City
City of Mesa
City of Somerton
City of Yuma
Electrical District No. 3, Pinal County, Arizona
Golden Shores Water Conservation District
Mohave County Water Authority
Mohave Valley Irrigation and Drainage District
Mohave Water Conservation District
North Gila Valley Irrigation and Drainage District
Town of Fredonia
Town of Thatcher
Town of Wickenburg
Salt River Project Agricultural Improvement and Power District
Unit "B" Irrigation and Drainage District
Wellton-Mohawk Irrigation and Drainage District
Yuma County Water Users' Association
Yuma Irrigation District
Yuma Mesa Irrigation and Drainage District

Other Interested Parties Participant Group

QuadState Local Governments Authority
Desert Wildlife Unlimited

California Participant Group

California Department of Fish and Wildlife
City of Needles
Coachella Valley Water District
Colorado River Board of California
Bard Water District
Imperial Irrigation District
Los Angeles Department of Water and Power
Palo Verde Irrigation District
San Diego County Water Authority
Southern California Edison Company
Southern California Public Power Authority
The Metropolitan Water District of Southern California

Nevada Participant Group

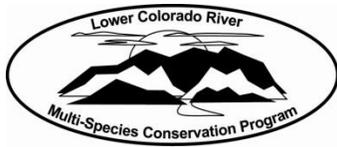
Colorado River Commission of Nevada
Nevada Department of Wildlife
Southern Nevada Water Authority
Colorado River Commission Power Users
Basic Water Company

Native American Participant Group

Hualapai Tribe
Colorado River Indian Tribes
Chemehuevi Indian Tribe

Conservation Participant Group

Ducks Unlimited
Lower Colorado River RC&D Area, Inc.
The Nature Conservancy



Lower Colorado River Multi-Species Conservation Program

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL) Basic Conceptual Ecological Model for the Lower Colorado River

Prepared by:

Christopher J.W. McClure, Ph.D., Elizabeth A. Johnson, and
Robert Unnasch, Ph.D.

Sound Science, LLC

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

September 2016

McClure, C.J.W., E.A. Johnson and R. Unnasch. 2016. Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL) Basic Conceptual Ecological Model for the Lower Colorado River. Submitted to the Bureau of Reclamation, Boulder City, Nevada, by Sound Science, LLC, Boise, Idaho.

ACRONYMS AND ABBREVIATIONS

CEM	conceptual ecological model
DBH	diameter at breast height
ha	hectare(s)
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
Reclamation	Bureau of Reclamation
SWFL	southwestern willow flycatcher (<i>Empidonax traillii extimus</i>)
USFWS	U.S. Fish and Wildlife Service

Symbols

>	greater than
≥	greater than or equal to
<	less than
≤	less than or equal to
%	percent
±	plus or min

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
Southwestern Willow Flycatcher Reproductive Ecology	2
Conceptual Ecological Model Purposes	2
Conceptual Ecological Model Structure for the SWFL.....	3
Chapter 2 – SWFL Life Stage Model	7
Introduction to the SWFL Life Cycle	7
SWFL Life Stage 1 – Nest.....	8
SWFL Life Stage 2 – Juvenile	8
SWFL Life Stage 3 – Breeding Adult.....	9
Life Stage Model Summary	10
Chapter 3 – Critical Biological Activities and Processes	11
Disease	12
Eating	12
Foraging	12
Molt.....	12
Nest Attendance	13
Nest Predation and Brood Parasitism	13
Nest Site Selection	13
Predation	13
Temperature Regulation.....	14
Chapter 4 – Habitat Elements	15
Anthropogenic Disturbance	17
Brood Size.....	17
Canopy Closure.....	18
Community Type	18
Conspecific Attraction	18
Distance to Occupied Patch	19
Diversity of Vegetation.....	19
Food Availability	20
Genetic Diversity and Infectious Agents	20
Humidity	21
Intermediate Structure.....	21

	Page
Linear Width of Patch.....	21
Local Hydrology.....	22
Matrix Community.....	22
Nest Predator and Cowbird Density.....	23
Parental Feeding Behavior.....	23
Parental Nest Attendance.....	23
Patch Size.....	24
Predator Density.....	24
Previous Year’s Use.....	24
Temperature.....	25
Tree Density.....	25
Chapter 5 – Controlling Factors.....	27
Fire Management.....	28
Grazing.....	28
Mechanical Thinning.....	28
Natural Thinning.....	29
Nuisance Species Introduction and Management.....	29
Pesticide/Herbicide Application.....	30
Planting Regime.....	30
Recreational Activities.....	30
Chapter 6 – Conceptual Ecological Model by Life Stage.....	33
SWFL Life Stage 1 – Nest.....	36
SWFL Life Stage 2 – Juvenile.....	43
SWFL Life Stage 3 – Breeding Adult.....	49
Chapter 7 – Causal Relationships Across All Life Stages.....	55
Anthropogenic Disturbance.....	56
Canopy Closure.....	56
Community Type.....	57
Food Availability.....	58
Intermediate Structure.....	58
Linear Width of Patch.....	59
Local Hydrology.....	60
Matrix Community.....	60
Nest Predator and Cowbird Density.....	60
Patch Size.....	61
Predator Density.....	62
Tree Density.....	62

	Page
Chapter 8 – Discussion and Conclusions	65
Most Influential Activities and Processes Across All Life Stages	65
Potentially Pivotal Alterations to Habitat Elements	66
Gaps in Understanding.....	68
Literature Cited.....	71
Acknowledgments.....	83

Tables

Table	Page
ES-1 Outcomes of each of the three life stages of SWFL	3
1 SWFL life stages and outcomes in the LCR ecosystem	10
2 Distribution of SWFL critical biological activities and processes among life stages (Xs indicate that the critical biological activity or process is applicable to that life stage.)	11
3 Distribution of SWFL habitat elements and the critical biological activities and processes they directly affect across all life stages	16
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 SWFL life history model.....	10
2 Diagram conventions for LCR MSCP conceptual ecological models.	35
3 SWFL life stage 1 – nest, basic CEM diagram.....	39
4 SWFL life stage 1 – nest, high- and medium-magnitude relationships.	41
5 SWFL life stage 2 – juvenile, basic CEM diagram. Only elements with connections within this life stage are presented.	45
6 SWFL life stage 2 – juvenile, high- and medium-magnitude relationships.	47
7 SWFL life stage 3 – breeding adult, basic CEM diagram.	51
8 SWFL life stage 3 – breeding adult, high- and medium- magnitude relationships.	53

Figures (continued)

Figure		Page
9	Most influential biological activities and processes affecting each life stage of SWFL. Only elements with high- or medium-magnitude connections are presented. The legend is provided on figure 2.	66
10	Habitat elements that directly affect the most influential biological activities and processes across all life stages of SWFL. Only elements with high- or medium-magnitude connections within this life stage are presented. The legend is provided on figure 2.	67

Attachments

Attachment	
1	Species Conceptual Ecological Model Methodology for the Lower Colorado River Multi-Species Conservation Program
2	Southwestern Willow Flycatcher 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 southwestern willow flycatcher (*Empidonax traillii extimus*) (SWFL). 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 SWFL ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure SWFL 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 SWFL 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.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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

- **Life stages** – These consist of the major growth stages and critical events through which an individual SWFL 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 other 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 a change in the second condition. The CEM method applied here assesses four variables for each causal relationship: (1) the character and direction of the effect, (2) the magnitude of the effect, (3) the predictability (consistency) of the effect, and (4) the certainty of a present scientific understanding of the effect. CEM diagrams and a linked spreadsheet tool document all information on the model components and their causal relationships.

CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

The SWFL conceptual ecological model addresses the SWFL 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 specifically address the biology of migratory the SWFL during migration or in its winter range.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

The most widely used sources of information for the SWFL conceptual ecological model are U.S. Fish and Wildlife Service (2002a), Reclamation (2004, 2008), BIO-WEST, Inc. (2005); Paradzick (2005), Paxton et al. (2007), (Moore 2007), Ellis et al. (2008), Sogge et al. (2010), Dobbs et al. (2012), Graber et al. (2012), and McLeod and Pellegrini (2013, 2014). 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 avian biologists. Our purpose is not to simply 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 SWFL 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 SWFL

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

The model distinguishes 9 critical biological activities or processes relevant to 1 or more of these 3 life stages and their outcomes, 22 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 22 habitat elements. Because the lower Colorado River (LCR) comprises a highly regulated system, the controlling factors 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 22 habitat elements identified across all life stages are: anthropogenic disturbance, brood size, canopy closure, community type, conspecific attraction, distance to occupied patch, diversity of vegetation, food availability, genetic diversity and infectious agents, humidity, intermediate structure, linear width of patch, local hydrology, matrix community, nest predator and cowbird density, parental feeding behavior, parental nest attendance, patch size, predator density, previous year's use, temperature, and tree density. The nine controlling factors identified across all habitat elements are: fire management, grazing, mechanical

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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:

- Eating, foraging, and predation are the most important critical biological activities and processes affecting survival of SWFL in all life stages (Fontaine and Martin 2006; Martin 2011). 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 SWFL in all life stages. For example, good nest sites may be in close proximity to more food, have fewer predators, and have fewer diseases present.
- Nest site selection is by far affected by the most habitat variables likely because this critical biological activity and process is not only the most researched but also because during the breeding season, nest site selection determines if the birds are present or not.
- Predation (including nest predation and brood parasitism) is also affected by a large number of habitat elements, including anthropogenic disturbance, canopy closure, community type, intermediate structure, linear width of patch, nest predator and cowbird density, patch size, predator density, and tree density, along with parental feeding behavior and parental nest attendance.
- Nest attendance is strongly affected by five habitat elements, including anthropogenic disturbance, brood size, humidity, predator density, and temperature. Anthropogenic disturbance may cause adult birds to flush and stay away from the nest (Burhans and Thompson, III 2001; U.S. Fish

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

and Wildlife Service 2002a). Brood size affects the amount of time SWFL must spend foraging versus attending the nest. Humidity and temperature affect nest attendance of birds along the LCR (Theimer et al. 2011). Predator density certainly affects predation rates (Schmidt et al. 2001).

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 SWFL survivorship and recruitment along the LCR. Specifically, the findings suggest a need to improve the understanding of:

- The effects of predation on juveniles and adults is poorly understood, whereas nest predation is better studied. This likely reflects the relative ease of studying depredation of nests versus free-flying birds. Since the persistence or population growth of SWFL populations is as sensitive to the survival of adults and juveniles as nest survival, more information regarding depredation on these life stages would be valuable.
- Anthropogenic disturbance has been noted to have a broad range of impacts on the ecology of birds (Francis and Barber 2013). Noise has been shown to affect foraging efficiency in many species but generally affects different species in different ways. SWFL are sensitive to disturbance of all kinds, and a better understanding of the impacts of all forms of anthropogenic disturbance would be valuable.
- The effects of disease, ecto-parasites, and endo-parasites have not been studied in SWFL or among passerine species inhabiting the LCR. Diseases have the potential to have dramatic impacts on populations (Robinson et al. 2010).
- The USFWS (2013) states that the matrix community might be an important aspect of SWFL habitat selection; however, little research has been conducted regarding the effect of matrix communities on the SWFL prey base or habitat use and nest site selection.

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 SWFL. 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 southwestern willow flycatcher (*Empidonax traillii extimus*) (SWFL). 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 SWFL ecology, the effects of specific stressors, the effects of specific management actions aimed at species habitat restoration, and the methods used to measure SWFL 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 SWFL population along the river and lakes of the lower Colorado River (LCR) and other protected areas along the LCR managed as SWFL 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 SWFL conceptual ecological model are U.S. Fish and Wildlife Service (USFWS) (2002a), Reclamation (2004, 2008), BIO-WEST, Inc. (2005), Paradzick (2005), Paxton et al. (2007), (Moore 2007), Ellis et al. (2008), Sogge et al. (2010), Dobbs et al. (2012), Graber et al. (2012), and McLeod and Pellegrini (2013, 2014). 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 avian biologists. The purpose of the conceptual ecological 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 SWFL, the purpose of the model, and introduces the underlying concepts and structure of the CEM. Succeeding chapters present and explain the model for SWFL along the LCR and evaluate the implications of this information for management, monitoring, and research needs.

SOUTHWESTERN WILLOW FLYCATCHER REPRODUCTIVE ECOLOGY

SWFL adults typically arrive on the breeding grounds between early May and early June. After-second-year males arrive earlier and set up territories before the females arrive (Sedgwick 2000; BIO-WEST, Inc. 2005; Reclamation 2008), whereas second-year males arrive at the same time as the females (Finch et al. 2002).

The female will choose a territory and then build a nest within a week of pair formation (Reclamation 2008). The nest is generally completed over a 4- to 7-day period (Finch et al. 2002). Incubation typically lasts 12–15 days, with most of the incubation and brooding being done by the female, while the male is more active in feeding the young after fledging (Finch et al. 2002; Sogge 2000). If adults fail to attain a territory or a mate, they may become “floaters” (adult birds that do not breed) within the population. Floaters are usually second-year males (Paxton et al. 2007).

Juveniles fledge between 12–15 days (Sogge 2000), and recently fledged young remain close to the nest for 3–5 days afterward (Finch et al. 2002). Juveniles will remain in the general vicinity of the nest and of parents for a couple of weeks and are fed by the parents during this time (Sedgwick 2000; Finch et al. 2002). During fall migration, juveniles generally leave the breeding grounds 1 or 2 weeks after the adults (Sedgwick 2000; BIO-WEST, Inc. 2005; Reclamation 2008). Studies of juvenile survival suggest that the survival of juvenile SWFL is lower than that of adults (Paxton et al. 2007; McLeod et al. 2008b; McLeod and Pellegrini 2013).

SWFL overwinter offsite and will return to the same breeding territory if they were successful the previous year (Paxton et al. 2007; McLeod and Pellegrini 2013). Typical breeding habitat consists of dense riparian vegetation characterized by overstory cottonwoods (*Populus fremontii*) and willows (*Salix gooddingii*). SWFL generally prefer patches that contain a mix of both dense areas for nest placement and open areas for foraging. SWFL are generalist insectivores, and the abundance and condition of the food supply affects adult health as well as the growth and development of the young during the nestling and juvenile stages.

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

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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.

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 SWFL

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

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Wildhaber et al. (2007), Kondolf et al. (2008), Burke et al. (2009), and Wildhaber (2011) to provide greater detail on causal linkages and outcomes and explicit demographic notation in the characterization of life-stage outcomes (McDonald and Caswell 1993). Attachment 1 provides a detailed description of the methodology. The resulting model is a “life history” model, as is common for CEMs focused on individual species (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 SWFL conceptual ecological model has five core components as explained further in attachment 1:

- **Life stages** – These consist of the major growth stages and critical events through which the individuals of a species must pass in order to complete a full life cycle.
- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals recruited to the next life stage (e.g., juvenile to adult), or the number of viable eggs 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; the rate (intensity) of the activities and processes, taken together, determine the rate of recruitment of individuals to the next life stage.
- **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

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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 water storage-delivery system design and operation (dam design, dam operations, and reservoir morphology), 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.

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 – SWFL 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 SWFL along the LCR on which to build the CEM.

INTRODUCTION TO THE SWFL LIFE CYCLE

Several demographic studies have resulted in the development of stage-based models of the life cycle of SWFL (Noon and Farnsworth 2000; Stoleson et al. 2000; Paxton et al. 2007; McLeod et al. 2008b; McLeod and Pellegrini 2013). Some of these demographic studies modeled the life cycle of SWFL based on two stages—hatch year and after hatch year (Noon and Farnsworth 2000; Stoleson et al. 2000). Other models used equations to estimate adult and juvenile survival as well as seasonal reproduction (Paxton et al. 2007; McLeod et al. 2008b; McLeod and Pellegrini 2013). During the development of the CEM of the life cycle of SWFL presented here, we drew heavily from the past models developed for SWFL while also considering what would be most useful to management. We therefore considered both the need to understand our model in the context of past work and the need to present the ecological information necessary to effectively manage habitats to support the critical biological activities and processes necessary to sustain SWFL populations.

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), and the SWFL is no exception (Noon and Farnsworth 2000; Stoleson et al. 2000; Paxton et al. 2007; McLeod et al. 2008b; McLeod and Pellegrini 2013). However, we treat the nest stage as separate from adult reproduction because nest success of the SWFL has been the subject of intense study, and the wealth of information learned from studies of SWFL nest success is best presented separately.

Further, we do not follow the framework of Noon and Farnsworth (2000) and Stoleson et al. (2000) of presenting hatch year and after hatch year stages. Instead, we examine the juvenile and breeding adult life stages of the SWFL following Paxton et al. (2007), McLeod et al. (2008b), and McLeod and Pellegrini (2013) because those stages more closely fit our definition of a life stage.

We also note that in a past version of this model we treated the egg and nestling stages as separate because they undergo different processes—e.g., eggs do not

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

need to eat or molt. We have here combined the egg and nestling stages into a nest stage because the both eggs and nestlings occupy the same nest; therefore, management focused on the nest will cover eggs and nestlings. Further, most research conducted on SWFL 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 incubation and brooding periods.

The migratory nature of the SWFL complicates its management. The LCR MSCP is mainly responsible for management of created habitat along the LCR where the species breeds, and we therefore focus on three life stages occurring within LCR MSCP lands—nest, juvenile, and breeding adult. SWFL management during migration and winter are certainly important but are outside of the scope of the LCR MSCP's responsibilities.

SWFL LIFE STAGE 1 – NEST

We consider the nest stage to be the first in the life cycle of the SWFL. It begins when the egg is laid and ends either when the young fledge or the nest fails. Eggs are usually laid in early to mid-June, and incubation lasts around 12 days, with all eggs in a clutch hatching within 2 days of each other (Finch et al. 2002; Reclamation 2008). Nestlings are generally present from mid-May through early August (Reclamation 2008) and fledging usually occurs 12–15 days after hatching (Finch et al. 2002; Reclamation 2008). Green et al. (2003) suggest that nest predation might be the most important factor affecting populations of the willow flycatcher in the Sierra Nevada, an assertion that, if true, makes the nest stage an especially important time in the life cycle of the SWFL. Further, Noon and Farnsworth (2000) found that reproduction—of which nest success is a huge factor—was the parameter that most affected the probability of population extinction. 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.

SWFL LIFE STAGE 2 – JUVENILE

The juvenile stage begins at fledging and ends when the bird returns to the breeding grounds the next year. For 3 to 5 days after fledging, juveniles will remain close to the nest, perhaps returning to and leaving the nest often (Finch et al. 2002). Juveniles will remain in the general vicinity of the nest and of parents for several weeks and are fed by the parents during this time (Sedgwick 2000; Finch et al. 2002). During fall migration, juveniles generally leave the breeding grounds 1 or 2 weeks after the adults (Sedgwick 2000; BIO-WEST, Inc.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

2005; Reclamation 2008). The life-stage outcome from the juvenile stage is the survival of the bird from fledging until the return to the breeding grounds the next calendar year. Studies of juvenile survival suggest that the survival of juvenile SWFL is lower than that of adults (Paxton et al. 2007; McLeod et al. 2008b; McLeod and Pellegrini 2013). Noon and Farnsworth (2000) found that survival of the first year of life was the second most influential parameter regarding population persistence.

SWFL LIFE STAGE 3 – BREEDING ADULT

The breeding 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. Note that we are considering all breeding individuals as adults, whereas some other studies separate between hatch year and after hatch year birds (Noon and Farnsworth 2000; Stoleson et al. 2000). Generally, adults arrive on the breeding grounds between early May and early June, with after-second-year males arriving earlier—and setting up territories before females arrive (Sedgwick 2000; BIO-WEST, Inc. 2005; Reclamation 2008). Second-year males generally arrive at the same time as females (Finch et al. 2002).

The female will choose a territory and then build a nest within a week of pair formation (Reclamation 2008). The nest is generally completed over a 4- to 7-day period (Finch et al. 2002). Most of the incubation and brooding is done by the female, although the male is more active in feeding the young after fledging (Finch et al. 2002). A pair may re-nest after a failed attempt, but clutch size decreases with each new nesting attempt (Finch et al. 2002). If an adult fails to attain a territory or a mate, they may become “floaters” within the population. Floaters are usually second-year males (Paxton et al. 2007).

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, the fecundity of adults involves the acts of pairing, site selection, nest building, and the production of eggs. As noted above, Noon and Farnsworth (2000) found that fecundity was the parameter that most influenced population persistence, although their estimates of fecundity included the nest stage.

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. During the post-breeding period, adults may prospect for potential future breeding areas or move into habitat types that differ from breeding areas and provide good conditions for

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

migratory staging (Vega Rivera et al. 2003; Paxton et al. 2007). 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 (Paxton et al. 2007), 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 SWFL 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.—SWFL 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

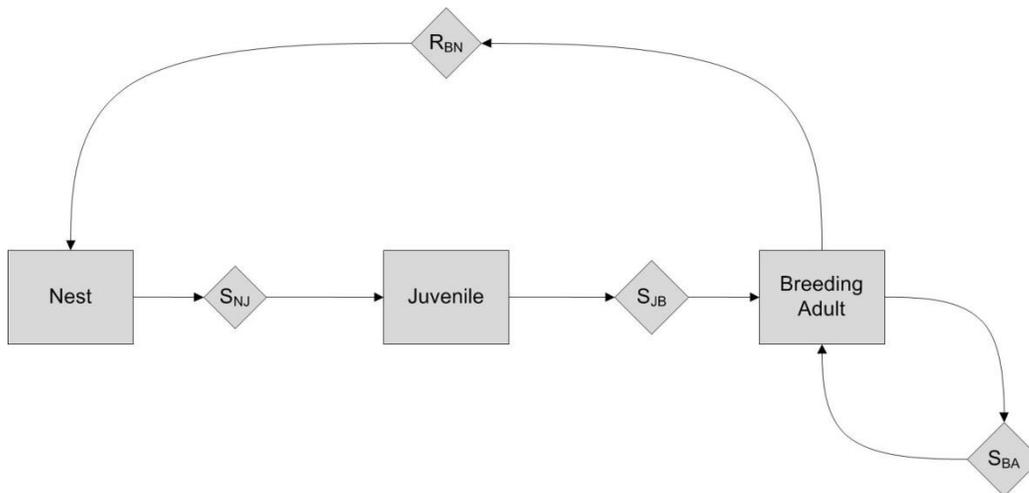


Figure 1.—Proposed SWFL life history model.

Squares indicate the life stages, and diamonds indicate the life-stage outcomes. S_{NJ} = survivorship rate, nest; S_{JB} = survivorship rate, juveniles; S_{BA} = 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 SWFL life stages. Some of these activities or processes differ in their details among life stages. However, grouping biological 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 SWFL 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		
Nest attendance			X
Nest predation and brood parasitism	X		
Nest site selection			X
Predation		X	X
Temperature regulation	X	X	X

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
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 USFWS (2002a), Reclamation (2004, 2008), BIO-WEST, Inc. (2005), Paradzick (2005), Paxton et al. (2007), (Moore 2007), Ellis et al. (2008), Sogge et al. (2010), Dobbs et al. (2012), Graber et al. (2012), and McLeod and Pellegrini (2013, 2014). The identification also integrates information from both older and more recent works as well as the expert knowledge of LCR MSCP avian biologists. The following paragraphs discuss the nine critical biological activities and processes in alphabetical order.

DISEASE

This process refers to diseases caused either by lack of genetic diversity or by infectious agents, including the effects of ecto- and endo-parasites. SWFL are known to be susceptible to a variety of diseases, although the effects of disease at a population level are not well understood and likely have a greater effect on small, isolated populations (Marshall and Stoleson 2000; Finch et al. 2002). SWFL in all life stages are conceivably susceptible to disease.

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 is determined by the foraging and provisioning rate of its parents.

FORAGING

SWFL are hawking insectivores that forage above the canopy, along edges of riparian patches, and within forest canopy openings (Finch et al. 2002; Reclamation 2004; USFWS 2013). Foraging is done by juveniles and adults, but it is important to note that foraging by the parents affects the provisioning rate to nestlings and nest attendance by adults. In addition, parents provide some food to the young for a time after fledging.

MOLT

Nestling SWFL must molt from natal down into juvenal plumage. All subsequent molts (both of juveniles into adult plumage and the annual adult molt) take place on the wintering grounds (not on LCR lands); therefore, this activity is not

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

included in the juvenile or breeding adult life stage but only applies to the nest stage (Unitt 1987). Molting is an energetically costly process that may make nestlings more susceptible to death when resources are scarce.

NEST ATTENDANCE

The female does most of the incubating and brooding, but the male helps with feeding of the young (Sedgwick 2000). 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 PREDATION AND BROOD PARASITISM

Nest predation and brood parasitism certainly affect the success of depredated or parasitized nests (Whitfield and Sogge 1999; McLeod and Pellegrini 2013). Brood parasitism is influenced by patch size and the relative proximity of the nest to a vegetation edge (Brodhead et al. 2007). These two processes have been combined for the nest stage because (1) cowbirds (*Molothrus ater*) 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, with males selecting territories and females selecting the actual nest site within that territory (Sedgwick 2000; Reclamation 2008). Nest site selection is important for reproductive success because nest success varies spatially as a result of vegetation characteristics, food availability, predator types and densities, hydrology, or unique events such as flooding (Paxton et al. 2007; McLeod and Pellegrini 2013).

PREDATION

Predation is a threat to SWFL in all life stages, and it obviously affects survival. For example, the primary cause of reproductive failure at the Elephant Butte Reservoir and along the LCR is nest predation (Ahlers and Moore 2009; McLeod and Pellegrini 2013). For this model, nest predation has been combined with brood parasitism and is treated as a separate critical process (see above). The predators of and rates of predation upon eggs and nestlings are much better understood (Theimer et al. 2011) than predation upon adults and even juveniles (Finch et al. 2002).

TEMPERATURE REGULATION

Temperature regulation is important for any organism inhabiting a region with temperatures as high as that along the LCR. Although overheating is possible during all life stages, most of the concern has been directed toward eggs and nestlings (Hunter et al. 1987a, 1987b; Rosenberg 1991). Adults can affect the temperature regulation of eggs and nestlings (during the nest stage) through their own behavior (incubation, brooding, or shading) and through nest placement.

Chapter 4 – Habitat Elements

Habitat elements consist of specific habitat conditions that ensure, allow, or interfere with critical biological activities and processes. Some elements, such as brood size and genetic diversity and infectious agents, are not traditionally considered aspects of habitat but are included in this section because of their effects on critical biological activities and processes.

Briefly, typical SWFL breeding habitat consists of patches at least 10 meters in width (Sogge et al. 2010) with dense riparian vegetation in the first 4 meters from the ground (Allison et al. 2003; McLeod et al. 2008a). These patches of breeding habitat often have standing water or saturated soils and may be interspersed with small openings in the canopy that are used for foraging (Sogge et al. 1997; Craig and Williams 1998; USFWS 2013). The USFWS (2013) states that SWFL are rarely found nesting in areas without willows, tamarisk (*Tamarix* spp.), or both. However, the structure of the vegetation is more important than the species composition, with both native and exotic-dominated community types being equivalent regarding habitat quality (Paxton et al. 2011; USFWS 2013).

This chapter identifies 22 habitat elements that affect 1 or more critical biological activities or processes across the 3 SWFL life stages. Some of these habitat elements differ in their details among life stages. For example, SWFL 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 SWFL, influence on similar species or species in similar habitats, or based upon the experience of the author and reviewers with SWFL or related species.

Table 3 lists the 22 habitat elements and the critical biological activities and processes that they *directly* affect across all SWFL life stages.

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 species that depredate SWFL during the juvenile and breeding adult stages.” The following paragraphs provide the full name for each habitat element and a detailed definition, addressing the elements in alphabetical order.

The most widely used sources of the information used to identify the habitat elements are USFWS (2002a), Reclamation (2004, 2008), BIO-WEST, Inc. (2005),

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 3.—Distribution of SWFL habitat elements and the critical biological activities and processes 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	Temperature regulation
Habitat element ↓							
Anthropogenic disturbance		X		X	X		
Brood size		X		X			
Canopy closure		X			X	X	X
Community type		X			X	X	
Conspecific attraction						X	
Distance to occupied patch						X	
Diversity of vegetation		X				X	
Food availability		X		X			
Genetic diversity and infectious agents	X						
Humidity				X		X	X
Intermediate structure					X	X	X
Linear width of patch					X	X	
Local hydrology							
Matrix community		X				X	
Nest predator and cowbird density					X		
Parental feeding behavior		X			X		
Parental nest attendance		X			X		X
Patch size					X	X	
Predator density				X	X	X	
Previous year's use						X	
Temperature				X		X	X
Tree density					X	X	

Note: There are no habitat elements that *directly* affect molt. Local hydrology affects critical biological activities and processes *indirectly* through other habitat elements of community type, food availability, humidity, and temperature.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Paradzick (2005), Paxton et al. (2007), (Moore 2007), Ellis et al. (2008), Sogge et al. (2010), Dobbs et al. (2012), Graber et al. (2012), and McLeod and Pellegrini (2013, 2014). 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 avian biologists.

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.)

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 recreational, land management, or scientific research activities, the presence of humans can disturb SWFL, causing changes in behavior that might ultimately affect survival. 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 SWFL to attract or find mates or defend territories. Further, noise might mask cues used in conspecific attraction, making it difficult for SWFL to find appropriate habitat. Noise can shift the foraging/vigilance tradeoff – either putting an individual at higher risk due to starvation or to predation (Ware et al. 2015). Noise can cause behavioral changes, physiological changes, and species diversity changes within an area. The effect of disturbance, including noise, by the presence of humans is better described for other species but has also been suggested for SWFL (USFWS 2002a). Anthropogenic disturbance is considered to be a habitat element, as it is an environmental characteristic or background condition with which a nesting or foraging flycatcher 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. Clutch 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 (see Gill 2007 and references therein), as well as other factors such as predator density (see “Predator and Cowbird Density”). Clutch size is also negatively correlated with distance to water (Peterson et al. 2015).

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 canopy closure of canopy vegetation in the vicinity of the SWFL nest site. Canopy closure of riparian vegetation, especially higher density in the upper canopy, has been shown to be important to SWFL. Dense vegetation around the nest may provide more optimal microclimate for thermoregulation (Rosenberg 1991; see Balluff 2012 for additional discussion) and camouflage from nest predators, although heterogeneity in canopy cover within a given patch or landscape may also be desirable (see “Diversity of Vegetation” below). Canopy closure may also affect the availability of food (Smith et al. 2006). Canopy cover is often related to tree density (James 1971; Rudnicki et al. 2004).

Moore (2007) concludes that canopy cover is not an important factor in SWFL breeding habitat because < 5 percent of SWFL sites contain trees in the upper canopy. Graf et al. (2002) state that SWFL prefer an open canopy. However, along the LCR, the median canopy closure at sites occupied by SWFL was 94 percent (McLeod and Pellegrini 2013). Further, the USFWS (2002a, 2013) lists a dense canopy as important for SWFL, citing several studies demonstrating higher canopy cover at occupied sites when compared to unoccupied sites (see attachment 2 for more details).

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 SWFL. Research shows that flycatchers are adaptable, able to use various types of native and non-native broadleaf deciduous habitats at different elevations (McLeod and Pellegrini 2013). Further, both native and exotic community types seem to be ecologically equivalent regarding the quality of SWFL breeding habitat (Paxton et al. 2007, 2011; USFWS 2013).

CONSPECIFIC ATTRACTION

Full name: **The propensity to nest near conspecifics.** SWFL display an aggregated nesting distribution, leading some to suggest that they prefer to nest near each other (USFWS 2002a; Brodhead 2005) and call for further research into the topic. The best evidence for conspecific attraction in SWFL comes from Brodhead (2005) who shows that an autocovariate, accounting for a clumped distribution, outperformed other aspects of habitat in describing the presence or

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL) Basic Conceptual Ecological Model for the Lower Colorado River

absence of breeding SWFL. The propensity for SWFL to nest near each other might explain the myriad of observations of apparently suitable habitat going unoccupied (see citations in Brodhead 2005). Playback of conspecific songs during settlement has been used as an effective tool to induce settlement by other species of songbirds to nesting areas selected by land managers (Schlossberg and Ward 2004; Ward and Schlossberg 2004). Therefore, playback of SWFL songs during early spring might be considered as a tool to induce settlement within the restoration areas along the LCR currently unused by SWFL.

DISTANCE TO OCCUPIED PATCH

Full name: **The linear distance of a given patch of riparian forest to the nearest occupied patch.** Movement of SWFL among patches of riparian habitat is most likely within 30–40 kilometers in central Arizona (Paxton et al. 2007) and up to 75 kilometers along the LCR (McLeod and Pellegrini 2013). Therefore, the probability that a given patch of riparian forest will be colonized by SWFL is influenced by its proximity to occupied habitat.

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). SWFL prefer nest sites with dense shrub (predominantly native willows) and canopy cover, which likely have high foliage height diversity.

Horizontal heterogeneity of vegetation within a territory or patch is also important for site use by SWFL (Hatten and Paradzick 2003; Paxton et al. 2007). Horizontal variation in the density of vegetation is important for SWFL because they require access to both dense and open areas during the breeding season. Dense areas provide vegetation to conceal nests and provide microclimate needed for egg and nestling development. Open areas facilitate foraging because SWFL are saltating flycatchers—they generally sit and wait at the edge of an opening and fly out to catch insects on the wing (Brodhead 2005; USFWS 2013). Ellis et al. (2008) determined the average distance from nests to canopy gaps at Roosevelt Lake to be approximately 8.4 meters in 2004 (prior to lake inundation). Therefore, although dense foliage is a classic characteristic of SWFL habitat, SWFL generally prefer patches that contain a mix of both dense areas for nest placement and open areas for foraging.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

We note here also that, because of the ephemeral nature of riparian habitat, a mosaic of patches of riparian forest of varying ages might be needed to ensure the persistence of SWFL within a given landscape (USFWS 2002a, 2013). A mosaic of varying ages of riparian forest would ensure that if some patches succeed into unsuitable seral stages or become unusable due to fire or inundation, other nearby suitable patches still would be available.

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 SWFL will encounter during each life stage as well as the density and spatial distribution of the food supply in proximity to the nest. SWFL are primarily insectivorous during the breeding season (Sedgwick 2000; Wiesenborn and Heydon 2007; Sogge et al. 2010). The abundance and condition of the food supply affects adult health as well as the growth and development of the young during the nestling and juvenile stages. In fact, in 2002 a drought at Roosevelt Lake, Arizona, reduced the SWFL prey base, causing almost complete reproductive failure (Durst et al. 2008). However, SWFL are generalist insectivores (Wiesenborn and Heydon 2007) and, therefore, may be able to adapt their diet to a variety of conditions—meaning that arthropod abundance and not diversity or the presence of specific taxa is most important for SWFL foraging (Durst et al. 2008).

GENETIC DIVERSITY AND INFECTIOUS AGENTS

Full name: **The genetic diversity of SWFL 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). SWFL exist as a complex of metapopulations that require periodic transfer of genetic material between them (Finch et al. 2002). The infectious agent component of this element refers to the spectrum of viruses, bacteria, fungi, ecto-parasites, and endo-parasites that individual SWFL are likely to encounter during each life stage. There is a wealth of knowledge regarding avian diseases and parasites that affect passerine birds within North America that indicates a large number of diseases (Morishita et al. 1999) can be difficult to detect (Jarvi et al. 2002) and can have differing effects on different species (Palinauskas et al. 2008). However, although there are many

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

infectious agents associated with SWFL, the effects of disease and other infectious agents are poorly understood (see USFWS 2002a and references therein).

HUMIDITY

Full name: **The amount of moisture in a habitat patch or nest site.** This element refers to the average relative humidity in the nesting habitat. Higher humidity levels may reduce the potential for egg desiccation and thermal stress and is important for egg and nestling survival in the more arid landscapes of the LCR region (McNeil et al. 2013). Further, SWFL are more likely to nest in sites with higher humidity (recommended mean diurnal relative humidity at nest sites = 53.0 ± 0.6 percent [McLeod et al. 2008a]).

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 intermediate level vegetation is a common characteristic of SWFL nesting habitat (Paxton et al. 2007; McLeod and Pellegrini 2013) and is perhaps one of the most often-listed characteristics of SWFL habitat. The USFWS (2002a, 2013) states that SWFL are most often found in areas with dense vegetation in the 4 meters above the ground. Moore (2007) found that shrub stem density did not differ between the nest and random plots in the Elephant Butte Reservoir Delta (mean = 3.64 per square meter), although nest plots had higher cover from 3 to 6 meters above the ground. A more dense intermediate structure may support a more diverse and abundant invertebrate food supply as well as provide protection or concealment from predators (see attachment 2 for more details).

LINEAR WIDTH OF PATCH

Full name: **The width of a patch of riparian habitat.** This element refers to the width of riparian habitat along a corridor. Flycatchers rarely breed in isolated habitat patches less than 10 meters in width (Sogge et al. 2010). Patch width may also affect the presence of nest parasites and other predators.

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 affect other aspects of habitat such as vegetation structure and abundance of arthropods. Wetter conditions might also provide cooler temperatures and more humid conditions necessary for egg and chick survival in desert systems (Rosenberg 1991).

The local hydrological conditions of a given patch might be the single most important determinant of SWFL habitat quality because it affects other aspects of habitat such as vegetation structure and abundance of arthropods (Ahlers and Moore 2009; Reclamation 2009; McLeod and Pellegrini 2013a; USFWS 2013). Wetter conditions might also provide cooler temperatures and more humid conditions necessary for egg and chick survival in these desert systems (Rosenberg 1991; McLeod and Pellegrini 2013). Being riparian obligates (Sogge et al. 2010), the distance to water is a strong predictor of the presence of nesting SWFL (Hatten and Paradzick 2003; Hatten et al. 2010) and is negatively correlated with SWFL clutch size (Peterson 2013).

The presence of surface water seems to be a strong driver of – or possibly a cue for – SWFL site selection (Paradzick 2005; Ahlers and Moore 2009; Sogge et al. 2010; McLeod and Pellegrini 2013; USFWS 2013), making local hydrological conditions during territory establishment especially important. Along the LCR, one-half of all sample points within SWFL territories were within 10 meters of water at the beginning of the nesting season (McLeod and Pellegrini 2013, 2014), and at Elephant Butte Reservoir Delta, 87 percent of the nests were found within 50 meters of surface water (Moore and Ahlers 2006). The average distance to water at Roosevelt Lake (in 2004, pre-inundation) was 187.6 meters (Ellis et al. 2008). Nesting SWFL selected the Salt River restoration project fields that retained water the longest. Fields are flood irrigated every 7–10 days throughout the breeding season (Salt River Project 2014). Therefore, the timing and duration of certain hydrological events (e.g., flooding) is important for site selection.

MATRIX COMMUNITY

Full name: **The type of habitat surrounding riparian patches used by flycatchers.** This element refers to the types of plant communities and land-use activities surrounding the riparian habitat patches used by SWFL. The USFWS (2013) states that the matrix community might be an important aspect of

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

SWFL habitat selection. Adjacent agricultural landscapes may have elevated pesticide/herbicide loads, which may affect foraging by adult and juvenile birds. A mosaic of natural communities might make exotic communities suitable because SWFL can forage in the matrix and the matrix might serve as a source area for arthropods (Durst 2004). Drost et al. (2003) state that mesquite (*Prosopis* sp.) and wetland habitat types might be more beneficial to SWFL as matrix communities rather than agricultural or urban areas, but little research has been conducted regarding the effect of matrix communities on the SWFL prey base or habitat use.

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 SWFL during the nest life stage or that 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 SWFL during different life stages, the density and spatial distribution of these fauna in the riparian habitat used by flycatchers, and the ways in which predator activity may vary in relation to other factors (e.g., intermediate structure, matrix community type, patch size and width, time of day, vegetation diversity, etc.) (Thompson, III 2007).

The effect of predator and cowbird density can have impacts more subtle than survival by altering breeding behavior, foraging behavior, nest site selection, and prey behavior (Lima 1998, 2009).

PARENTAL FEEDING BEHAVIOR

Full name: **The ability and behavior of parents to feed and care for nestlings and juveniles after they fledge from the nest.** This element refers to the capacity of both parents to provision food for recently fledged birds. Juveniles continue to be fed by the parents for several weeks after fledging. The feeding rate is dependent upon food availability and the number of young in the brood. This rate influences the amount of food and 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

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

parents to share nesting and brood-rearing responsibilities until fledging. It is affected by food availability, the presence of predators and competitors, and the ability to thermoregulate.

PATCH SIZE

Full name: **The size of riparian habitat patches.** This element refers to the areal extent of a given patch of riparian vegetation. Although the average patch size may differ between riverine and reservoir systems (Paxton et al. 2007), the patch size affects the number of breeding pairs that an area can support as well as the density of brood parasites, competitors, and predators. Brodhead (2005) found that SWFL are more likely to occupy larger patches. However, in general, patch size is not a limiting factor in SWFL habitat selection as long as riparian patches are at least 10 meters in width—SWFL have been observed breeding in patches ranging in size from 0.01–70 hectares (USFWS 2013).

PREDATOR DENSITY

Full name: **The abundance and distribution of species that depredate SWFL during the juvenile and breeding 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 SWFL during the juvenile or adult life stages. The variables of this element include the species and size of the fauna that prey on SWFL during different life stages, the density and spatial distribution of these fauna in the riparian habitat used by flycatchers, and the ways in which predator activity may vary in relation to other factors (e.g., intermediate structure, matrix community type, patch size and width, time of day, vegetation diversity, etc.) (Thompson, III 2007).

The effect of predator density can have impacts more subtle than survival by altering breeding behavior, foraging behavior, nest site selection, and prey behavior (Lima 1998, 2009).

PREVIOUS YEAR'S USE

Full name: **The location of the previous year's breeding attempt and whether or not that attempt was successful.** SWFL are more likely to return to the same territory after a successful breeding attempt (Paxton et al. 2007; McLeod and Pellegrini 2013). Individuals that return to a successful territory tend to do well, and those that abandon an unsuccessful territory are more successful in a new location the next year (Paxton et al. 2007).

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). Thermoregulation is necessary for survival of chicks and adults, and flycatchers nest in areas with moderated temperature ranges (McLeod et al. 2008a). High temperatures typical of the LCR region in the summer can kill eggs and stress young in the nest (Hunter et al. 1987b; Rosenberg 1991).

TREE DENSITY

Full name: **The stem density of trees reported as the number of trees per acre.** The greater the tree and/or shrub density, the greater the likelihood of denser vegetative cover. Moore (2007) found that tree stem density was higher in nest versus random plots in the Elephant Butte Reservoir Delta. Tree density is likely highly correlated with canopy closure and total vegetation density (see “Diversity of Vegetation,” above).

Chapter 5 – Controlling Factors

Controlling factors consist of environmental conditions and dynamics, both natural and anthropogenic, which significantly affect the abundance, spatial and temporal distributions, and quality of critical habitat elements. These may also significantly and 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 shows 10 habitat elements that are not directly affected by any controlling factor (brood size, conspecific attraction, distance to occupied patch, diversity of vegetation, genetic diversity and infectious agents, humidity, 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 →	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
Habitat element ↓									
Anthropogenic disturbance			X					X	
Brood size	N/A*								
Canopy closure	X		X	X	X		X	X	
Community type	X	X			X		X	X	X
Conspecific attraction	N/A*								
Distance to occupied patch	N/A*								
Diversity of vegetation	N/A*								
Food availability					X	X			
Genetic diversity and infectious agents	N/A*								
Humidity	N/A*								
Intermediate structure	X	X	X		X		X	X	
Linear width of patch	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*								
Temperature	N/A*								
Tree density	X		X	X	X		X	X	

FIRE MANAGEMENT

This factor addresses any fire management (whether prescribed fire or fire suppression) that could affect SWFL or their habitat. Effects may include creation of habitat that supports or excludes SWFL, a reduction in the food supply of invertebrates, or support of species that pose threats to SWFL such as predators, competitors, or carriers of infectious agents. Although typically not a major threat in most riparian habitats, severe wildfires have affected flycatcher breeding sites in the past decade (USFWS 2002a; Graber et al. 2007; Ellis et al. 2008). The USFWS (2013) specifically recommends fire management for the recovery of SWFL populations. Climate change is also projected to affect fire frequency along the LCR (USFWS 2013).

GRAZING

This factor addresses the grazing activity on riparian habitats along the LCR and in surrounding areas that could affect SWFL 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 2002b). (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, 2003) reports 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. (Note: SWFL were not one of the species monitored during this study but likely would benefit from similar management strategies.)

Grazing activity may also influence other controlling factors, such as nuisance species introduction and management, by increasing cowbird presence or by spreading non-native grass seeds into riparian habitat (Goguen and Mathews 2001; Bartuszevige and Endress 2008; Tucson Audubon 2012).

MECHANICAL THINNING

This factor addresses the active removal of vegetation from areas within the LCR region. Effects may include the creation of habitat that supports or excludes SWFL or support of species that pose threats to SWFL such as predators,

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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 it can be implemented on a broad scale with larger and more complete transition. Mechanical thinning always increases the level of anthropogenic disturbance, especially noise, within the habitat.

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 profile needed by SWFL.

NUISANCE SPECIES INTRODUCTION AND MANAGEMENT

This factor addresses the intentional or unintentional introduction of nuisance species (animals and plants) and their control that affects SWFL survival and reproduction. Nuisance species may infect, prey on, compete with, or present alternative food resources for SWFL during one or more life stages, cause other alterations to the riparian food web that affect SWFL, or affect physical habitat features such as intermediate structure and canopy or shrub cover. For example, although SWFL successfully nest in sites dominated by invasive tamarisk, larger monocultures of tamarisk may negatively affect habitat in other ways (e.g., by altering soil chemistry, habitat structure, and/or the arthropod community, etc.) (Di Tomaso 1998; Tamarisk Coalition 2009).

The complicated nature of the relationship between tamarisk and SWFL is highlighted by another introduced species—the tamarisk beetle (*Diorhabda carinulata*). The tamarisk beetle was introduced to the region in St. George Utah on the Virgin River to control invasive tamarisk (Bateman et al. 2013; McLeod and Pellegrini 2013), and the beetle has since spread. Although tamarisk control is an important management activity, defoliation of tamarisk due to beetle infestation causes decreases in humidity and cover along with increases in temperature (Bateman et al. 2013), thereby degrading areas dominated by tamarisk as habitat for SWFL (McLeod and Pellegrini 2013). Any control measures to remove tamarisk-dominated habitat used for nesting by flycatchers need to include rapid replacement with other dense, preferably native vegetation (Paxton et al. 2007).

PESTICIDE/HERBICIDE APPLICATION

This factor addresses biocide applications that may occur on or adjacent to riparian habitat of the LCR region. The use of pesticides/herbicides was listed as a potential threat to SWFL by the USFWS (USFWS 2002a). Effects may include sublethal poisoning of SWFL via ingestion of treated insects, pollution of runoff into wetland habitats that are toxic to prey of SWFL, 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).

RECREATIONAL ACTIVITIES

This factor addresses the disturbance to SWFL from recreational or 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, etc.) as well as the frequency and intensity of those activities. The impacts may consist of direct disturbance of SWFL 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). The USFWS (2002a, 2013) lists recreational activities as being a threat to SWFL and suggests that it be addressed by management.

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 SWFL.

WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATION

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

It is important to note that both riverine and palustrine areas provide habitat for SWFL. The dynamic nature of a free-flowing river creates a mosaic of riparian habitats, and thus, a natural flow regime might be beneficial to the SWFL (Graf et al. 2002; USFWS 2002a, 2013; Graber et al. 2007). Although alteration of the natural flow of rivers is generally considered detrimental to SWFL habitat, currently some of the largest SWFL populations are within the drawdown zones of reservoirs (Sogge et al. 2010). Fluctuations in water levels within reservoirs can mimic—to some extent—the natural destruction and regeneration of riparian vegetation associated with natural flowing systems (Paxton et al. 2007; Reclamation 2009). SWFL will also use riparian vegetation created by sewage and agricultural drainages as well as irrigation canals (USFWS 2002a).

Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains three sections, each presenting the CEM for a single SWFL 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 the river and lakes of the LCR and other protected areas managed as SWFL habitat and thus address 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

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
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.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

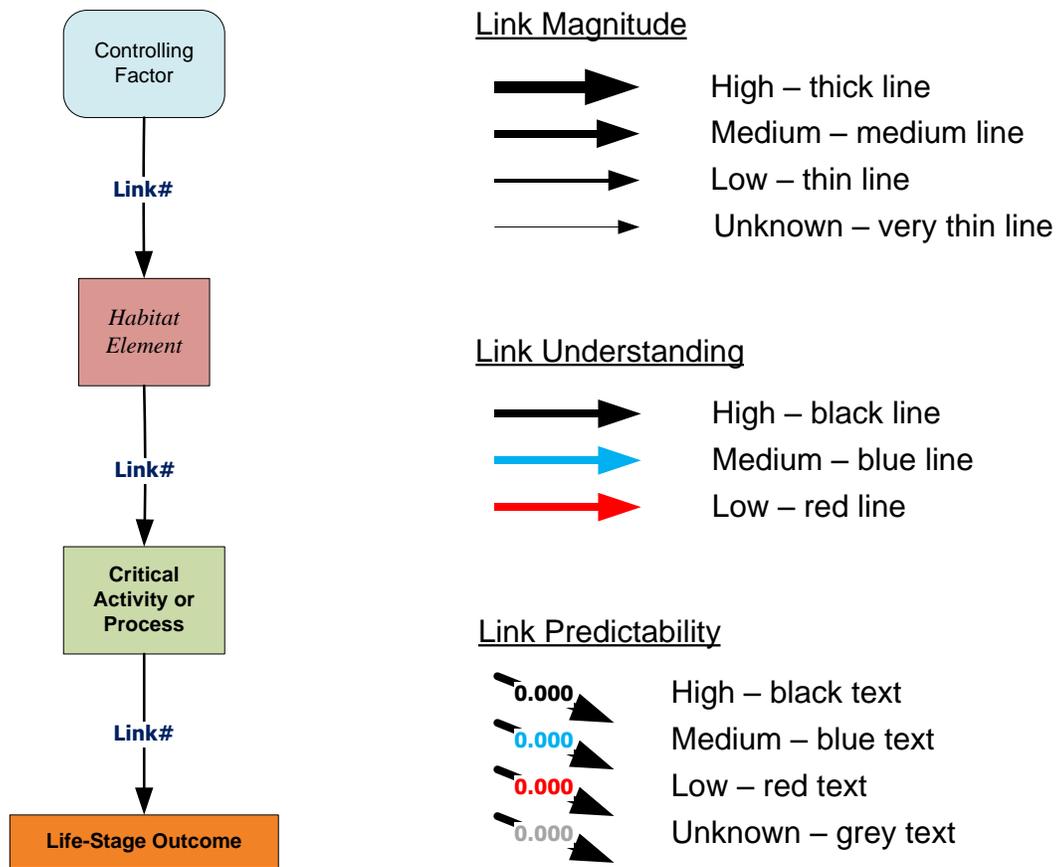


Figure 2.—Diagram conventions for LCR MSCP conceptual ecological models.

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.

SWFL 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, ordered here as they appear on the following figures:

1. **Disease** – Although the literature does not emphasize disease as affecting population levels of SWFL, we still feel that disease bears mentioning, and it has been recommended as an area for further research (Paxton et al. 2007).

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

2. **Eating** – The nestling must eat to maintain metabolic processes.

The CEM recognizes brood size and parental nest attendance as habitat elements affecting eating (feeding young).

3. **Nest Predation and Brood Parasitism** – Both nest predation and brood parasitism affect the survival of a nest and are affected by similar habitat elements. Brood parasitism has been identified as a threat to SWFL (Marshall and Stoleson 2000), although it likely only threatens small populations (Finch et al. 2002). We have therefore combined nest predation and brood parasitism into one process for this stage.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, intermediate structure, linear width of patch, nest predator and cowbird density, parental nest attendance, patch size, and tree density as habitat elements affecting nest predation and brood parasitism.

4. **Molt** – The nestling must molt into juvenal plumage.

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

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
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, humidity, intermediate structure, parental nest attendance, and temperature as habitat elements directly affecting temperature regulation.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
 Basic Conceptual Ecological Model for the Lower Colorado River

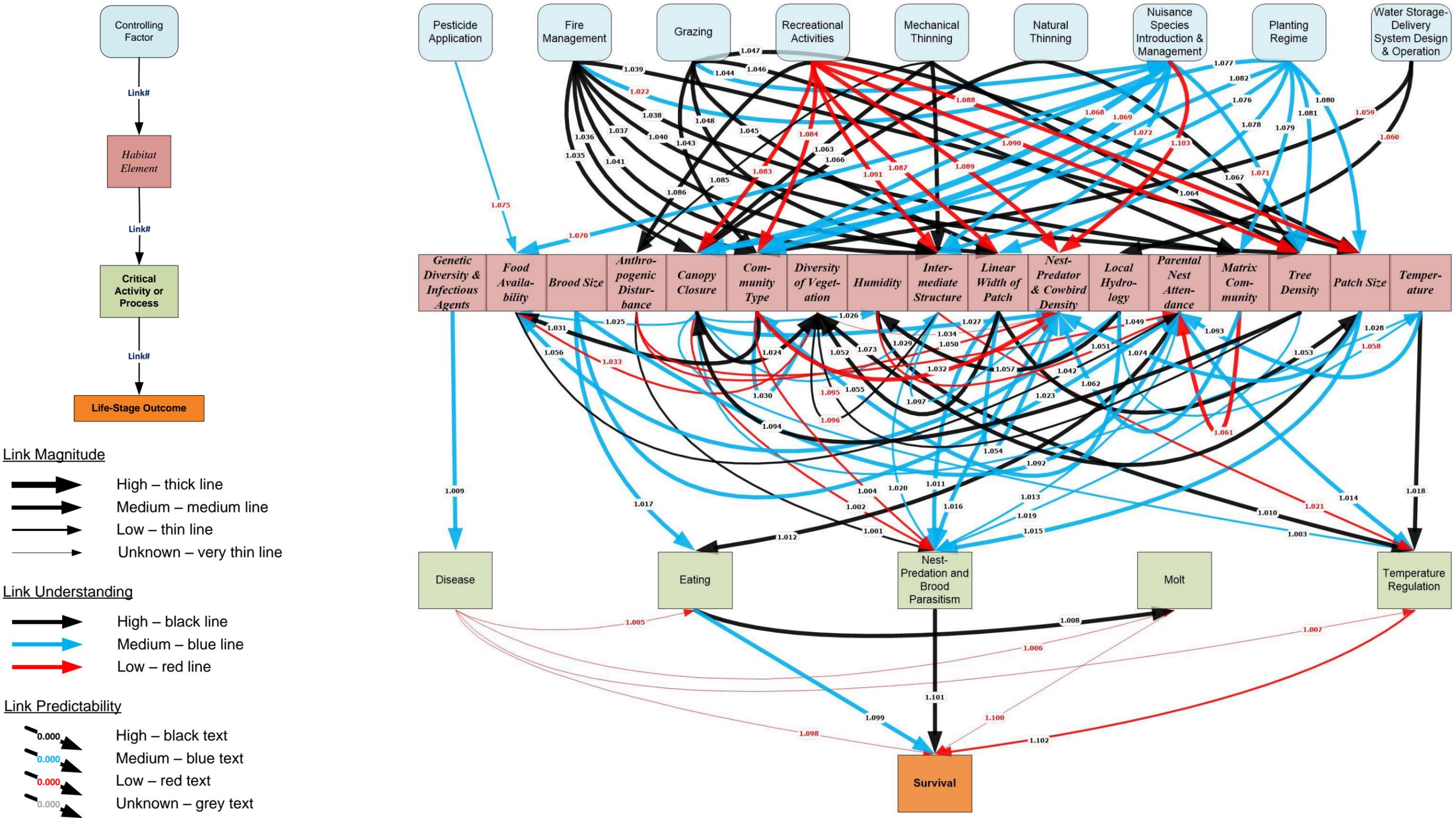


Figure 3.—SWFL life stage 1 – nest, basic CEM diagram.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
 Basic Conceptual Ecological Model for the Lower Colorado River

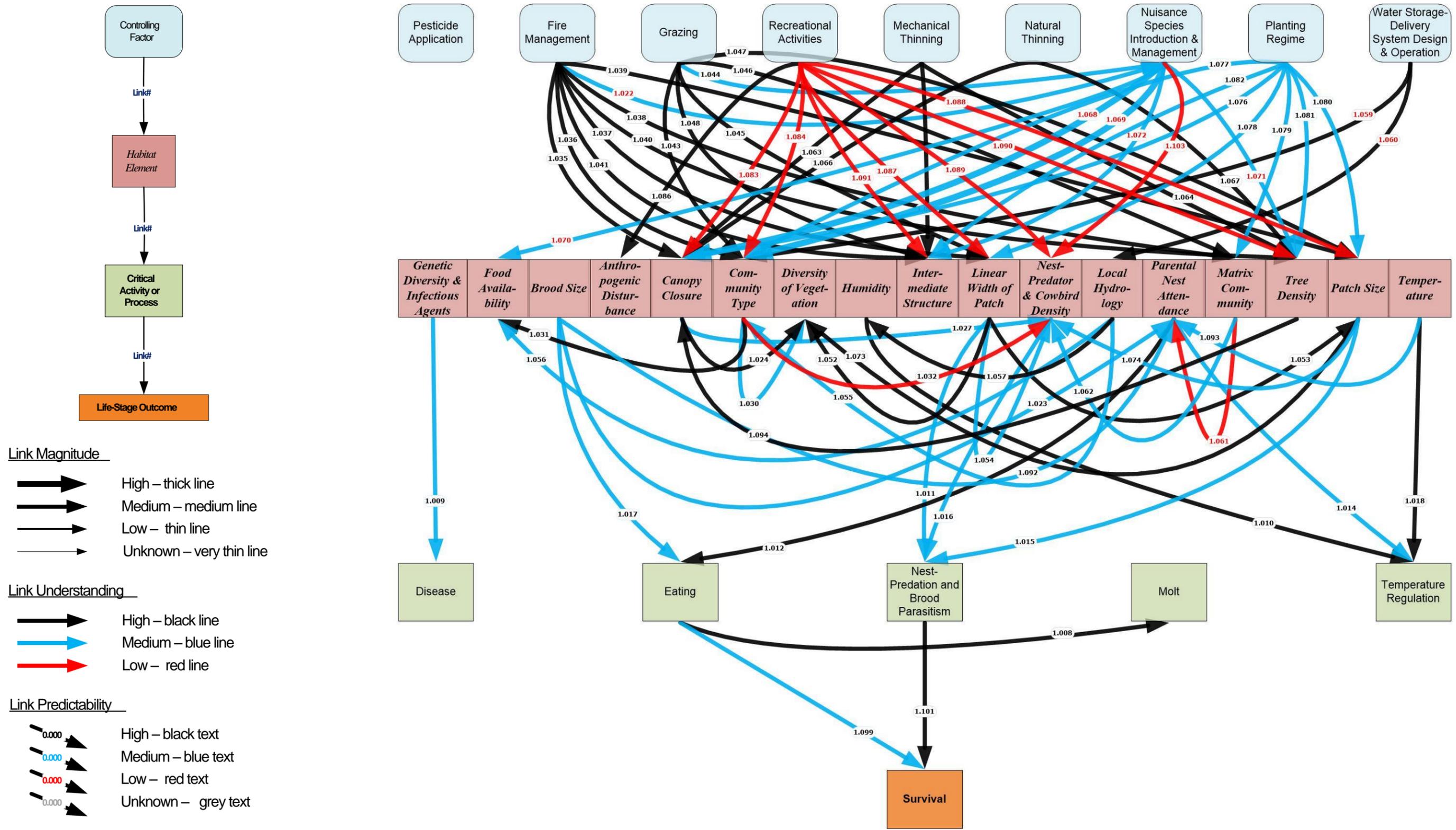


Figure 4.—SWFL life stage 1 – nest, high- and medium-magnitude relationships.

SWFL LIFE STAGE 2 – JUVENILE

The juvenile stage begins at fledging and ends when the bird engages in breeding activities, usually the following year. 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 four (of nine) critical biological activities and processes for this life stage, ordered here as they appear on the following figures:

1. **Disease** – Although the literature does not emphasize disease as affecting population levels of SWFL, we still feel that disease bears mentioning, and it has been recommended as an area for further research (Paxton et al. 2007).

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 parent survival.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, diversity of vegetation, food availability, matrix community, and parental feeding behavior as habitat elements affecting foraging. Predator density affects foraging indirectly via predation, but nothing is known about rates for juveniles. In addition, disease can also affect the foraging efficiency of a juvenile, but it is not known to what extent.

3. **Predation** – Brood parasitism is no longer a threat to the survival of SWFL; therefore, it is no longer included with predation.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, intermediate structure, linear width of patch, parental feeding behavior, patch size, predator density, and tree density as habitat elements affecting predation.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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

The CEM recognizes canopy closure, humidity, intermediate structure, and temperature as habitat elements directly affecting temperature regulation.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River

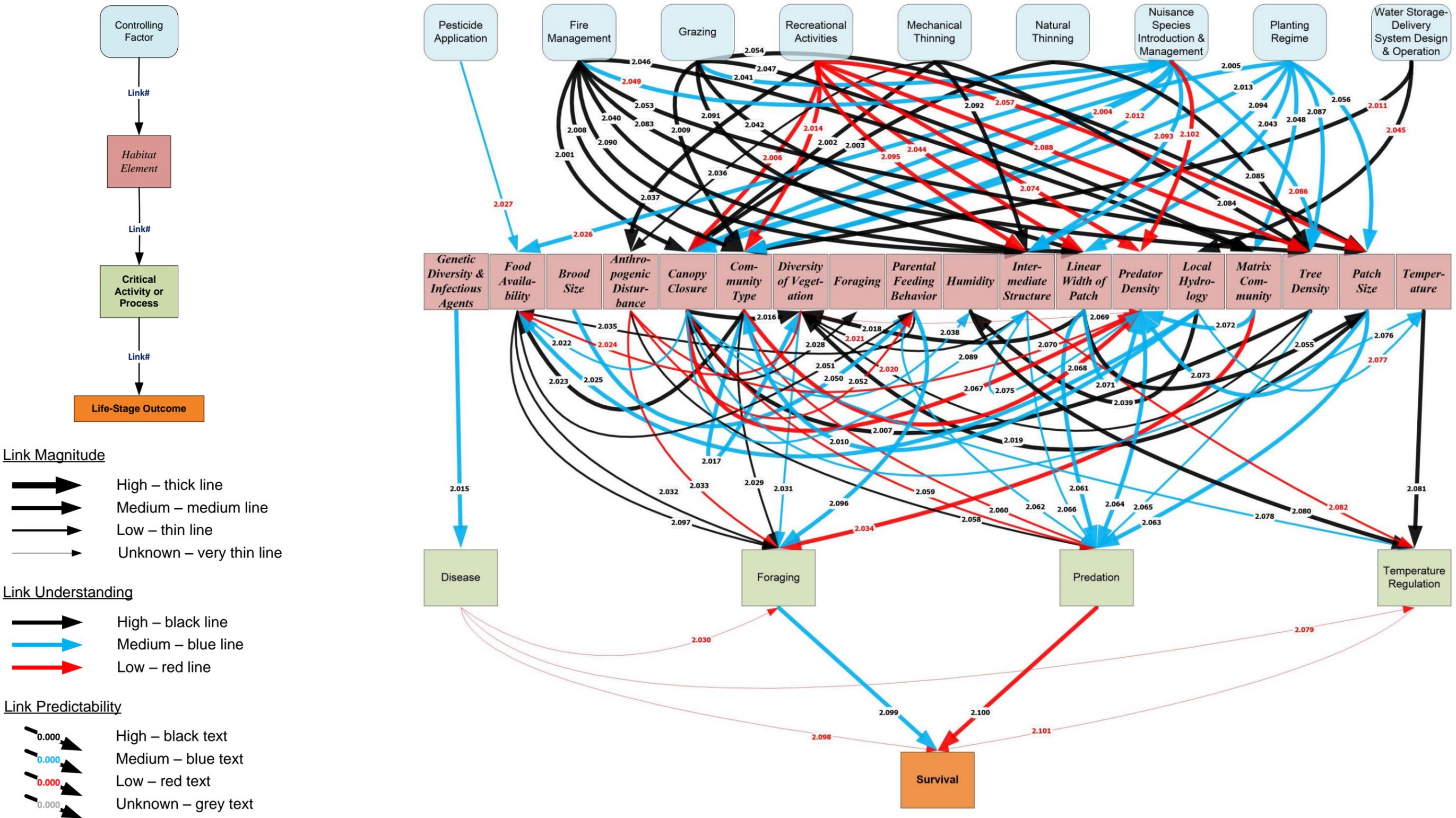


Figure 5.—SWFL life stage 2 – juvenile, basic CEM diagram. Only elements with connections within this life stage are presented.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
 Basic Conceptual Ecological Model for the Lower Colorado River

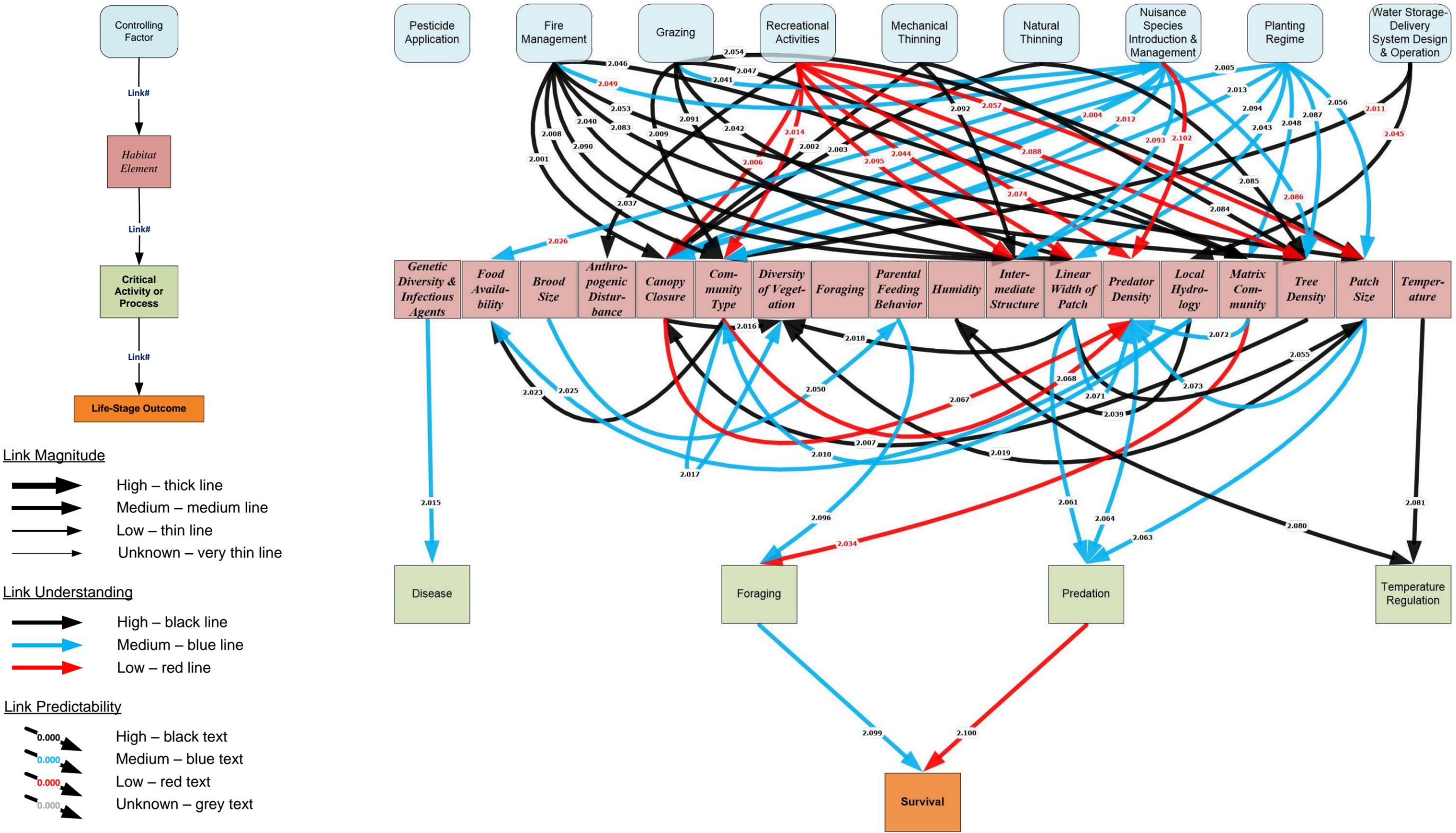


Figure 6.—SWFL life stage 2 – juvenile, high- and medium-magnitude relationships.

SWFL 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 six (of nine) critical biological activities and processes for this life stage, ordered here as they appear on the following figures:

1. **Disease** – Although the literature does not emphasize disease as affecting population levels of SWFL, we still feel that disease bears mentioning, and it has been recommended as an area for further research (Paxton et al. 2007).

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.

The CEM recognizes anthropogenic disturbance, brood size, canopy closure, community type, diversity of vegetation, food availability, and the matrix community as affecting foraging.

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

The CEM recognizes anthropogenic disturbance, canopy closure, community type, intermediate structure, linear width of patch, patch size, predator density, and tree density as habitat elements affecting predation.

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

The CEM recognizes anthropogenic disturbance, brood size, humidity, predator density, and temperature as habitat elements affecting nest attendance.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

5. **Nest Site Selection** – This process includes both territory establishment and the placement of nests. 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 nests, thereby affecting breeding success.

The CEM recognizes anthropogenic disturbance, canopy closure, community type, conspecific attraction, distance to occupied patch, diversity of vegetation, humidity, intermediate structure, linear width of patch, matrix community, patch size, predator density, previous year's use, temperature, and tree density as habitat elements affecting nest site selection.

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

The CEM recognizes canopy closure, humidity, intermediate structure, and temperature as habitat elements directly affecting temperature regulation.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River

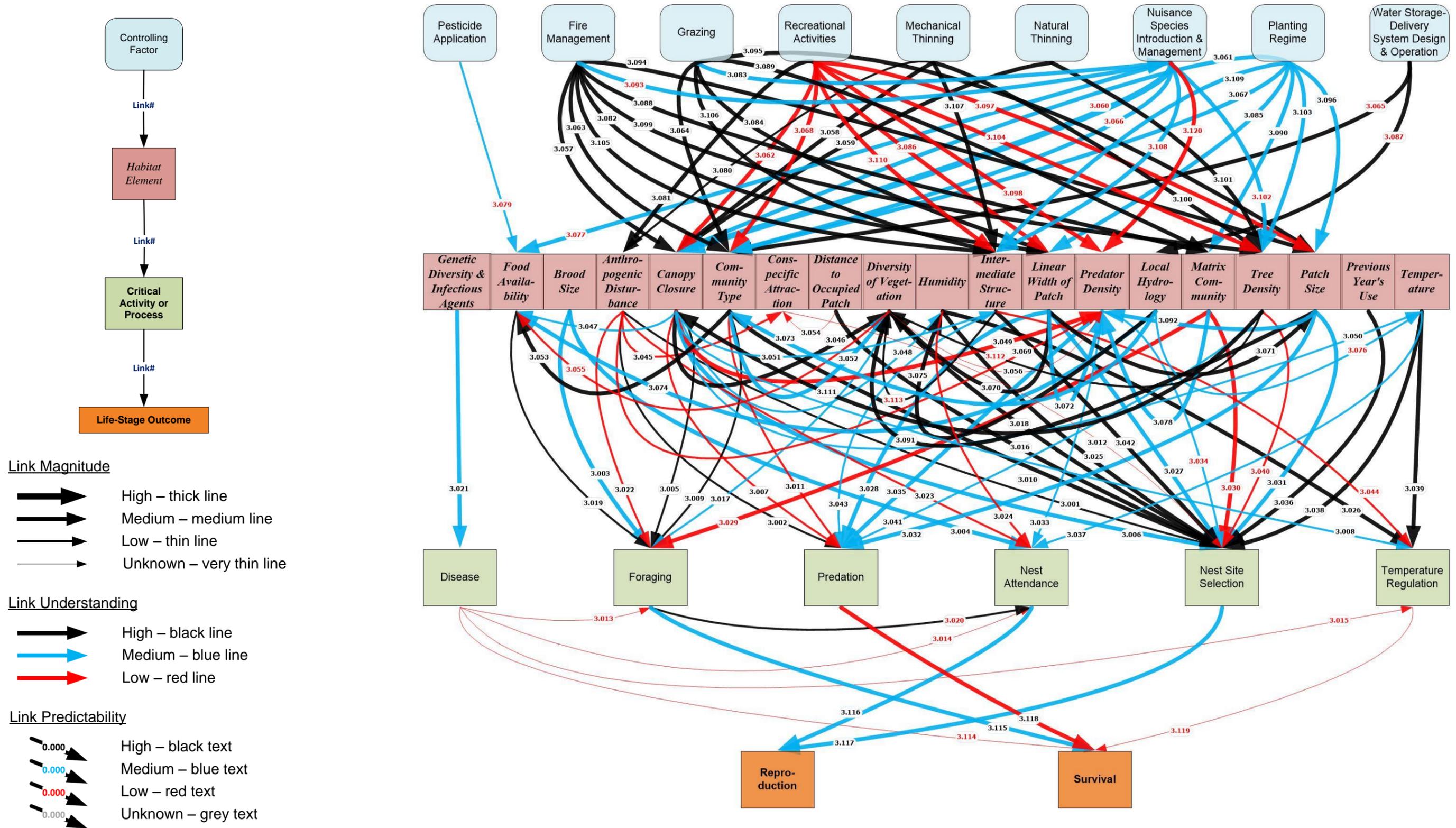


Figure 7.—SWFL life stage 3 – breeding adult, basic CEM diagram.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River

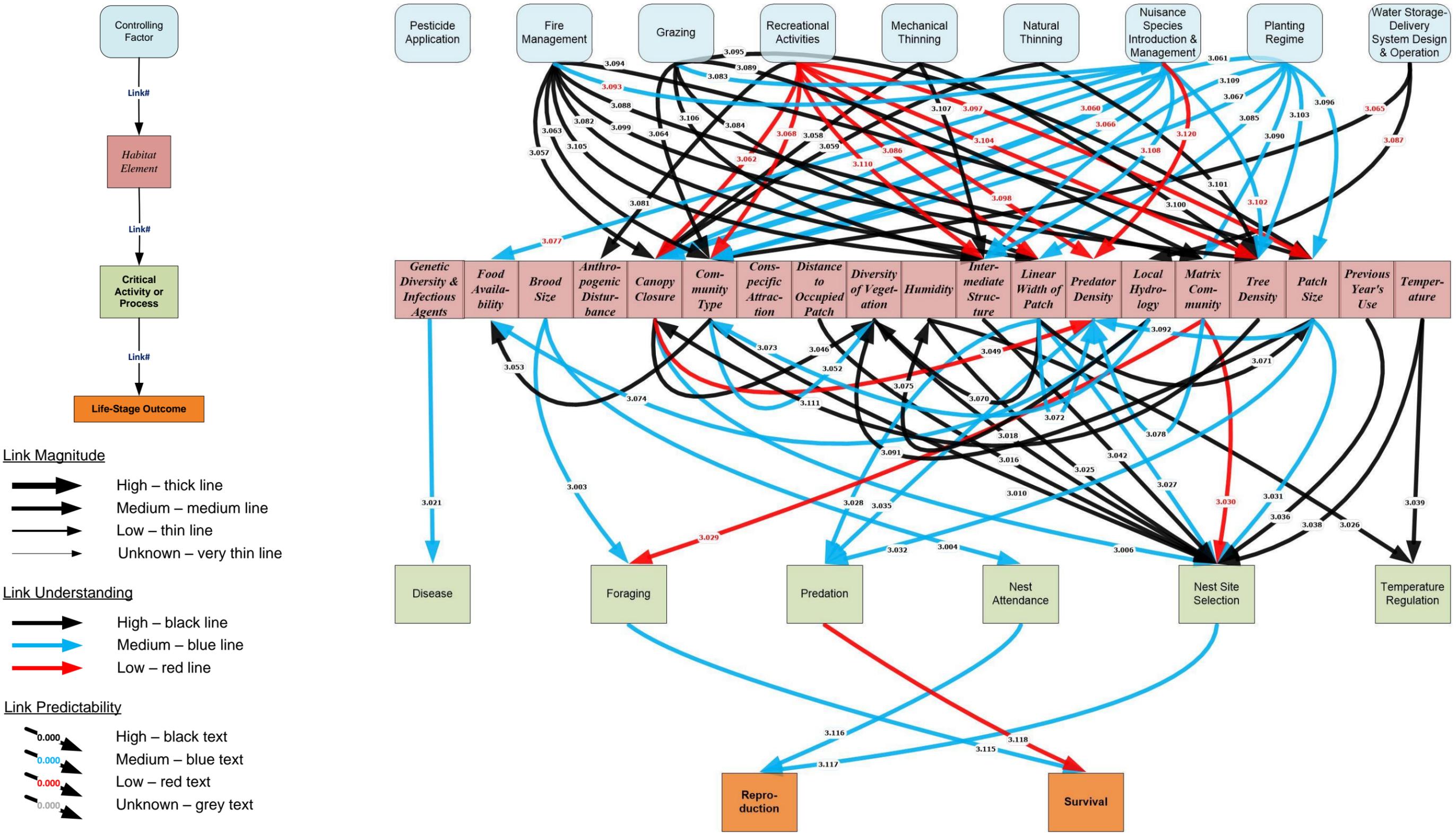


Figure 8.—SWFL life stage 3 – breeding adult, high- and medium-magnitude relationships.

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 22 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 High = **H**, Medium = **M**, Low = **L** follows:

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

Controlling factor →									
Habitat element affected ↓	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			L					M	
Brood size	N/A*								
Canopy closure	M		M	M	H		M	M	
Community type	M	M			M		M	M	M
Conspecific attraction	N/A*								
Distance to occupied patch	N/A*								
Diversity of vegetation	N/A*								
Food availability					M	L			
Genetic diversity and infectious agents	N/A*								
Humidity	N/A*								
Intermediate structure	M	M	M		M		M	M	
Linear width of patch	M	M					M	M	
Local hydrology									M
Matrix community	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*								
Temperature	N/A*								
Tree density	M		M	M	M		M	M	

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

ANTHROPOGENIC DISTURBANCE

All activities involving humans increase anthropogenic disturbance, and the controlling factors that affect anthropogenic disturbance include mechanical thinning and recreational activities.

Mechanical thinning can also increase noise levels at a site, which may affect nesting birds when done during the breeding season.

Increases in recreation should lead to more humans present in riparian areas, and this can increase noise levels depending on the activity. The intensity of this link is likely proportional. Decisions regarding management of recreational activities can affect large areas, but the effects of a change in recreational activities on anthropogenic disturbance would last far less than a decade. Noise is an inherently short-term phenomenon, unless it is of a repeated nature (e.g., campsites, off-highway vehicle trails, or nearby roads).

CANOPY CLOSURE

The controlling factors that directly affect canopy closure include fire management, mechanical thinning, natural thinning, nuisance species introduction and management, planting regime, and recreational activities. Fire management, mechanical thinning, and recreational activities will generally reduce canopy closure, whereas the effects of nuisance species introduction and management and the planting regime depend on the management actions and species involved.

Fire management is usually implemented over large areas and can have great effects on canopy closure. 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 would be done at the patch level, with effects lasting until the canopy grows back, and can be as intense as managers wish.

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

Nuisance species can change the structure of entire communities, with lasting effects (Di Tomaso 1998). Although the effects are experienced at a patch level, invasive species can spread across entire regions, and their effects can last decades.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Planting regimes have the ability to greatly affect canopy closure. 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.

The potential impact of recreational activities on canopy closure is great, although it depends on the type and duration of the activity and how well it is managed. Decisions regarding management of recreational activities can affect large areas, but the dynamic nature of both human activity and riparian communities means that effects of recreation (depending on type, intensity, and effectiveness of management) will likely last less than a decade when appropriately managed.

COMMUNITY TYPE

The controlling factors that directly affect community type include fire management, grazing, nuisance species introduction and management, planting regime, recreational activities, and water storage-delivery system design and operation. It is not possible to state whether the effects of controlling factors are positive or negative.

Fire management can have great effects on the type of vegetation growing in a given patch 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.

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

Nuisance or invasive species can change the structure of entire communities (Sogge et al. 2008), with lasting effects.

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.

The USFWS (2002a) states that recreational activities can affect the species composition of riparian forest.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Water storage and flow regimes can affect vegetation communities used by SWFL (Marshall and Stoleson 2000; Nilsson and Svedmark 2002) in part by altering the hydrologic regime. The effects of water storage spread over large scales, but the effects of changes in flow regimes likely last less than a decade.

FOOD AVAILABILITY

The controlling factors that directly affect the food available to a SWFL are nuisance species introduction and management and pesticide/herbicide application.

Nuisance species can change the arthropod community, and the effects of nuisance species can spread across entire regions and result in a permanent transformation of the landscape.

The magnitude of the effect of pesticides/herbicides depends on many factors, but the potential magnitude is very high. 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.

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 management, grazing, mechanical thinning, and recreational activities 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 management can have great effects on the type of vegetation growing in a given patch 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.

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.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

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

Nuisance species introduction and management can change the structure of entire communities, with lasting effects. Although effects are experienced at a patch level, 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.

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

LINEAR WIDTH OF PATCH

The controlling factors that directly affect the width of a given patch of riparian vegetation include fire management, grazing, planting regime, and recreational activities. Fire management, grazing, and recreational activities will generally reduce the width of a riparian patch, whereas the effects of the planting regime depend on the management actions and species involved.

Fire management can have great effects on the width of a given patch 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.

Grazing affects many aspects of vegetation structure and composition (Kauffman et al. 1997). Grazing activity can heavily affect the width of a patch and is often implemented over large and long scales. However, the dynamic nature of riparian communities means that effects of grazing will likely last less than a decade.

Planting regimes have the ability to greatly affect the linear width of a patch. 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.

The USFWS (2002a) states that recreational activities can affect riparian vegetation. Therefore, the potential impact of recreational activities on SWFL habitat is great, although it depends on the type and duration of the activity and how well it is managed. Decisions regarding management of recreational

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

activities can affect large areas, but the dynamic nature of both human activity and riparian communities means that effects of recreation will likely last less than a decade.

LOCAL HYDROLOGY

The only controlling factor affecting local hydrology is 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 affects water levels and therefore the distance to water, soil moisture, and other hydrological conditions. Water storage and flow regimes can affect vegetation communities and food abundance (Nilsson and Svedmark 2002). The effects of water storage spreads over large scales, but the effects of changes in flow regimes likely will be short term in nature unless a complete transformation of the habitat occurs.

MATRIX COMMUNITY

The controlling factors that directly affect the matrix community include fire management, grazing, and planting regime. It is not possible to assign a direction on the effects of controlling factors.

Fire management can have great effects on the matrix community 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.

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

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

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.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Nuisance species control efforts (or lack of them) can affect the densities of cowbirds, affecting SWFL nest success. Some studies have shown predator and cowbird presence differs among community types, native, and non-native habitats (Schmidt et al. 2005).

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, 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 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 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 riparian forests, although it depends on the activity. However, the dynamic nature of both human activity and riparian communities means that effects of recreation will likely be short term in nature after the completion of 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. However, any change in the composition of the predator community can have a large and lasting impact on the SWFL population (Lima 2009).

Nuisance species introduction and management that affects the community type may alter predator densities. 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, invasive species can spread across entire regions, and their effects can last decades if not resulting in a permanent transformation.

Recreational activities can influence 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).

TREE DENSITY

The controlling factors that directly affect tree density include fire management, mechanical thinning, natural thinning, nuisance species introduction and management, planting regime, and recreational activities. Fire management, mechanical/natural thinning, and recreational activities will generally reduce tree 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 (Engstrom et al. 1984) and can destroy SWFL 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 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 tree density, it works on small scales, creating forest gaps. The effect only lasts until the vegetation grows back.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Nuisance species introduction and management can change the structure of entire communities, with lasting effects. Although the effects are experienced at a patch level, 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.

The potential impact of recreational activities on tree density in SWFL 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 this assessment in three ways by posing three questions: (1) which critical biological activities and processes most strongly affect the individual 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 STAGES

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

- Eating, foraging, and predation are the most important critical biological activities and processes affecting survival of SWFL in all life stages (Fontaine and Martin 2006; Martin 2011). 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 in all life stages. For example, good nest sites may be in close proximity to more food, have fewer predators, and have fewer diseases present.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River

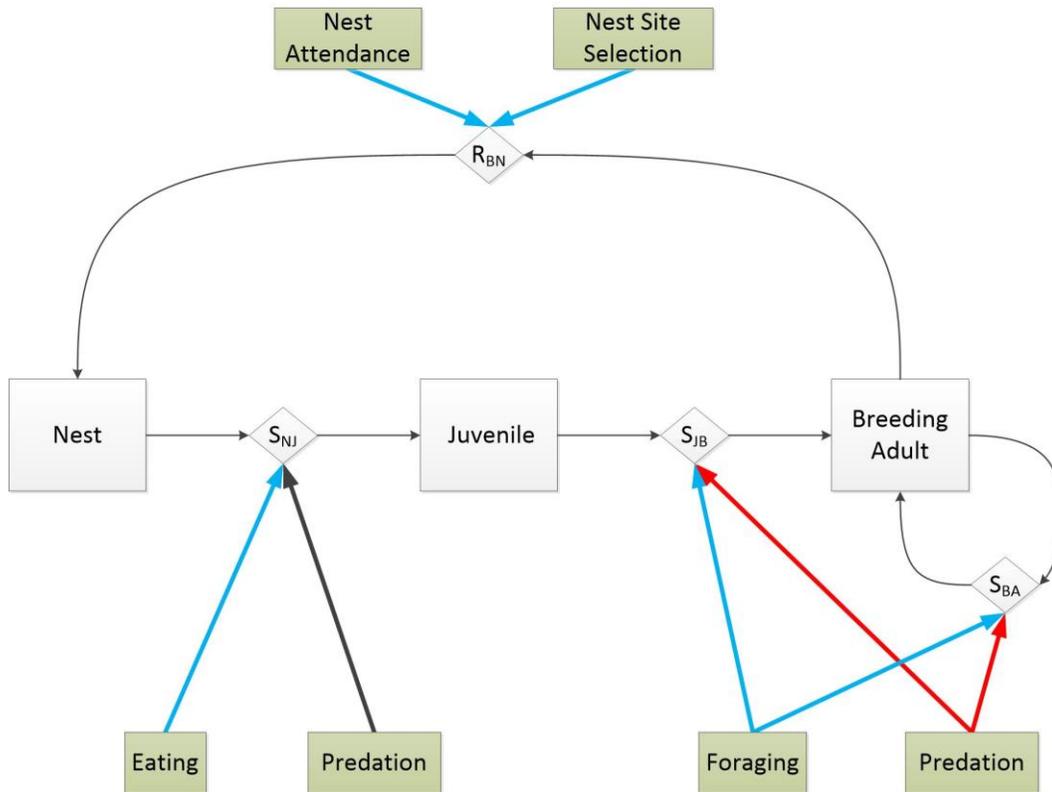


Figure 9.—Most influential biological activities and processes affecting each life stage of SWFL. Only elements with high- or medium-magnitude connections are presented. The legend is provided on figure 2.

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 and process is not only the most researched among those on figure 10, but also during the breeding season, nest site selection determines if the birds are present or not.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
 Basic Conceptual Ecological Model for the Lower Colorado River

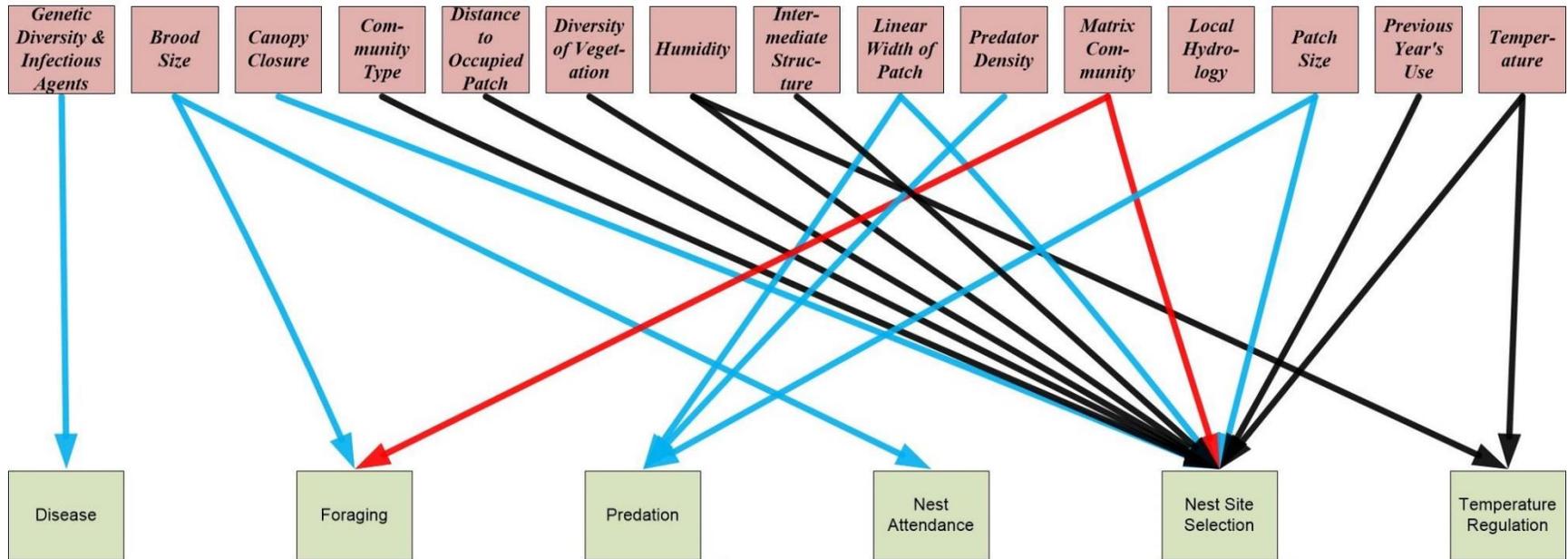


Figure 10.—Habitat elements that directly affect the most influential biological activities and processes across all life stages of SWFL. Only elements with high- or medium-magnitude connections within this life stage are presented. The legend is provided on figure 2.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Predation (including nest predation and brood parasitism) is also affected by a large number of habitat elements, including anthropogenic disturbance, canopy closure, community type, intermediate structure, linear width of patch, nest predator and cowbird density, patch size, predator density, and tree density, along with parental feeding behavior and parental nest attendance.
- Nest attendance is strongly affected by five habitat elements, including anthropogenic disturbance, brood size, humidity, predator density, and temperature. Anthropogenic disturbance may cause adult birds to flush and stay away from the nest (Burhans and Thompson, III 2001; USFWS 2002a). Brood size affects the amount of time SWFL must spend foraging versus attending the nest. Humidity and temperature affects nest attendance of birds along the LCR (Theimer et al. 2011). Predator density certainly affects predation rates (Schmidt et al. 2001).

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 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.

- The effects of predation on juveniles and adults is poorly understood, whereas nest predation is better studied. This likely reflects the relative ease of studying depredation of nests versus free-flying birds. Since the persistence or population growth of SWFL populations is as sensitive to the survival of adults and juveniles as nest survival, more information regarding depredation on these life stages would be valuable.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Anthropogenic disturbance has been noted to have a broad range of impacts on the ecology of birds (Francis and Barber 2013). Noise has been shown to affect foraging efficiency in many species but generally affects different species in different ways. SWFL are sensitive to disturbance of all kinds, and a better understanding of the impacts of all forms of anthropogenic disturbance would be valuable.
- The effects of disease, ecto-parasites, and endo-parasites have not been studied in the SWFL or among passerine species inhabiting the LCR. Diseases have the potential to have dramatic impacts on populations (Robinson et al. 2010).
- The USFWS (2013) states that the matrix community might be an important aspect of SWFL habitat selection, however little research has been conducted regarding the effect of matrix communities on SWFL prey base or habitat use and nest site selection.

This list of uncertainties is not meant to be exhaustive but only to highlight topics the literature identifies as potentially pivotal to SWFL recruitment along the LCR and to identify important gaps in these publications. They are not in any way to be considered guidance for Reclamation or LCR MSCP, nor are these knowledge gaps expected to be addressed under the program.

LITERATURE CITED

- Ahlers, D. and D. Moore. 2009. A Review of Vegetation and Hydrologic Parameters Associated with the Southwestern Willow Flycatcher – 2002 to 2008. Elephant Butte Reservoir Delta NM. U.S. Department of the Interior, Bureau of Reclamation, Fisheries and Wildlife Resources, Denver, Colorado.
- Allendorf, F.W. and R.F. Leary. 1986. Heterozygosity and fitness in animals *in* M.E. Soule (editor). Conservation Biology. Sinauer, Sunderland, Massachusetts. pp. 57–76.
- Allison, L.J., C.E. Paradzick, J.W. Rourke, and T.D. McCarthy. 2003. A characterization of vegetation in nesting and non-nesting plots for southwestern willow flycatchers in central Arizona. *Studies in Avian Biology* 26:81–90.
- Balluff, T. 2012. Soil Hydrology and Microclimate Conditions in Occupied Southwestern Willow Flycatcher and Yellow-billed Cuckoo Habitat. U.S. Department of the Interior, Bureau of Reclamation, Lower Colorado Regional Office, Boulder City, Nevada.
- Bangert, R., S.M. Ferrier, L. Evans, K. Kennedy, K.C. Grady, E. Hersch-Green, G.J. Allan, and T.G. Whitham. 2013. The proportion of three foundation plant species and their genotypes influence an arthropod community: restoration implications for the endangered southwestern willow flycatcher. *Restoration Ecology* 21(4):447–456.
- Barber, J.R., K.R. Crooks, and K.M. Fristrup. 2010. The costs of chronic noise exposure for terrestrial organisms. *Trends in Ecology & Evolution* 25:180–189.
- Bartuszevige, A.M. and B.A. Endress. 2008. Do ungulates facilitate native and exotic plant spread? *Journal of Arid Environments* 72:904–913.
- Bateman, H.L., P.L. Nagler, and E.P. Glenn. 2013. Plot-and landscape-level changes in climate and vegetation following defoliation of exotic saltcedar (*Tamarix* sp.) from the biocontrol agent *Diorhabda carinulata* along a stream in the Mojave Desert (USA). *Journal of Arid Environments* 89:16–20.
- BIO-WEST, Inc. 2005. Colorado River Backwaters Enhancement Species Profile Report. Bureau of Reclamation, Lower Colorado Regional Office, Boulder City, Nevada.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Boyle, S.A. and F.B. Samson. 1985. Effects of nonconsumptive recreation on wildlife: a review. *Wildlife Society Bulletin* 13:110–116.
- Brodhead, K.M. 2005. The influence of riparian-canopy structure and coverage on the breeding distribution of the southwestern willow flycatcher. Montana State University, Bozeman, Montana.
- Brodhead, K.M., S.H. Stoleson, and D.M. Finch. 2007. Southwestern willow flycatchers (*Empidonax traillii extimus*) in a grazed landscape: factors influencing brood parasitism. *The Auk* 124(4):1213-1228.
- Bureau of Reclamation (Reclamation). 2004. Lower Colorado River Multi-Species Conservation Program, Volume II: Habitat Conservation Plan, Final. Sacramento, California.
- _____. 2008. Species Accounts for the Lower Colorado River Multi-Species Conservation Program. Bureau of Reclamation, Lower Colorado Region, Boulder City, Nevada.
- _____. 2009. Elephant Butte Reservoir Five-Year Operational Plan – Biological Assessment. U.S. Department of the Interior, Bureau of Reclamation, Albuquerque Area Office, Albuquerque, New Mexico.
- Burhans, D.E. and F.R. Thompson, III. 2001. Relationship of songbird nest concealment to nest fate and flushing behavior of adults. *The Auk* 118(1):237–242.
- Burke M., K. Jorde, and J.M. Buffington. 2009. Application of a hierarchical framework for assessing environmental impacts of dam operation: changes in hydrology, channel hydraulics, bed mobility and recruitment of riparian trees in a western North American river. *Journal of Environmental Management* S224–S236.
- Craig, D. and P.L. Williams. 1998. Willow flycatcher (*Empidonax traillii*) in The Riparian Bird Conservation Plan: A Strategy for Reversing the Decline of Riparian-associated Birds in California. California Partners in Flight.
- Di Tomaso, J.M. 1998. Impact, biology, and ecology of saltcedar (*Tamarix* spp.) in the southwestern United States. *Weed Technology* 12:326–336.
- DiGennaro, B., D. Reed, C. Swanson, L. Hastings, Z. Zachary, M. Healey, S. Siegel, S. Cantrell, and B. Herbold. 2012. Using conceptual models in ecosystem restoration decision making: an example from the Sacramento-San Joaquin River Delta, California. *San Francisco Estuary and Watershed Science* 10(3).

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Dobbs, R.C., M. Huizinga, C.N. Edwards, and R.A. Fridell. 2012. Status, Reproductive Success, and Habitat Use of Southwestern Willow Flycatchers on the Virgin River, Utah, 2008–2011. Publication Number 12-36. Utah Division of Wildlife Resources, Salt Lake City, Utah.
- Drost, C.A., E.H. Paxton, M.K. Sogge, and M.J. Whitfield. 2003. Food habits of the southwestern willow flycatchers during the nesting season. *Studies in Avian Biology* 26:96–103.
- Durst, S.L. 2004. Southwestern Willow Flycatcher Potential Prey Base and Diet in Native and Exotic Habitats. M.Sc. thesis. Northern Arizona University, Flagstaff, Arizona.
- Durst, S.L., T.C. Theimer, E.H. Paxton, and M.K. Sogge. 2008. Age, habitat, and yearly variation in the diet of a generalist insectivore, the southwestern willow flycatcher. *The Condor* 110:514–525.
- Ellis, L.A., D.M. Weddle, S.D. Stump, H.C. English, and A.E. Graber. 2008. Southwestern Willow Flycatcher Final Survey and Nest Monitoring Report 2008, Research Technical Guidance Bulletin. Arizona Game and Fish Department, Phoenix, Arizona.
- Engstrom, R.T., R.L. Crawford, and W.W. Baker. 1984. Breeding bird populations in relation to changing forest structure following fire exclusion: a 15-year study. *Wilson Bulletin* 96:437–450.
- Erdelen, M. 1984. Bird communities and vegetation structure: I. Correlations and comparisons of simple and diversity indices. *Oecologia* 61:277–284.
- Etterson, M.A., S.N. Ellis-Felege, D. Evers, G. Gauthier, J.A. Grzybowski, B.J. Mattsson, L.R. Nagy, B.J. Olsen, C.M. Pease, M. Post van der Burg, and A. Potvien. 2011. Modeling fecundity in birds: conceptual overview, current models, and considerations for future developments. *Ecological Modelling* 222:2178–2190.
- Finch, D.M., S.I. Rothstein, J.C. Boren, W.L. Graf, J.L. Holechek, B.E. Kus, R.M. Marshall, M.M. Pohl, S.J., Sferra, M.K. Sogge, J.C. Stromberg, B.A. Valentine, M.J. Whitfield, and S.O. Williams. 2002. Final Recovery Plan of the Southwestern Willow Flycatcher (*Empidonax traillii extimus*), Albuquerque, New Mexico: U.S. Fish and Wildlife Service, Region 2.
- Fischenich C. 2008. The application of conceptual models to ecosystem restoration. EMRRP–EBA–01. U.S. Army Engineer Research and Development Center, Vicksburg, Mississippi. 23 p.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Fontaine, J.J. and T.E. Martin. 2006. Parent birds assess nest predation risk and adjust their reproductive strategies. *Ecology Letters* 9:428–434.
- Francis, C.D. and J.R. Barber. 2013. A framework for understanding noise impacts on wildlife: combining ethology, ecology and bioacoustics to address an urgent conservation priority. *Frontiers in Ecology and Evolution* 11:305–313.
- Gill, F.B. 2007. *Ornithology*. W.H. Freeman and Company, New York.
- Goguen, C.B. and N.E. Mathews. 2001. Brown-headed cowbird behavior and movements in relation to livestock grazing. *Ecological Applications* 11(5):1533–1544.
- Graber, A.E., D.M. Weddle, H.C. English, S.D. Stump, H.E. Telle, and L.A. Ellis. 2007. Southwestern Willow Flycatcher 2006 Survey and Nest Monitoring Report. Nongame and Endangered Wildlife Program. Technical Report 249. Arizona Game and Fish Department, Phoenix.
- Graber, A.E., T.J. Koronkiewicz, and J.L. Granger. 2012. Southwestern Willow Flycatcher Surveys and Nest Monitoring along the Gila River between Coolidge Dam and South Butte, 2011. Annual summary report submitted to U.S. Bureau of Reclamation, Glendale, Arizona. Flagstaff, Arizona: SWCA Environmental Consultants.
- Graf, W.L., J. Stromberg, and B. Valentine. 2002. Rivers, dams, and willow flycatchers: a summary of their science and policy connections. *Geomorphology* 47:169–188.
- Green, G., H. Bombay, and M. Morrison. 2003. Conservation Assessment of the Willow Flycatcher in the Sierra Nevada. U.S. Department of Agriculture, Forest Service, Region 5, Sacramento, California.
- Hatten, J.R. and C.E. Paradzick. 2003. A multiscaled model of southwestern willow flycatcher breeding habitat. *The Journal of Wildlife Management*:774–788.
- Hatten, J.R., E.H. Paxton, and M.K. Sogge. 2010. Modeling the dynamic habitat and breeding population of southwestern willow flycatcher. *Ecological Modelling* 221:1674–1686.
- Hunter, W.C., B.W. Anderson, and R.D. Ohmart. 1987a. Avian community structure changes in a mature floodplain forest after extensive flooding. *The Journal of Wildlife Management* 51:495–502.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- _____. 1987b. Status of breeding riparian-obligate birds in southwestern riverine systems. *Western Birds* 18:10–18.
- James, F.C. 1971. Ordinations of habitat relationships among breeding birds. *The Wilson Bulletin* 83:215–236.
- Jennings, S.B., N.D. Brown, and D. Sheil. 1999. Assessing forest canopies and understory illumination: canopy closure, canopy cover and other measures. *Forestry* 72:59–74.
- Kauffman, J.B., R.L. Beschta, N. Otting, and D. Lytjen. 1997. An ecological perspective of riparian and stream restoration in the western United States. *Fisheries* 22:12–24.
- Kokos, S. 2014. Bureau of Reclamation, Boulder City, Nevada personal communication.
- Kondolf, G.M., P. Angermeier, K. Cummins, T. Dunne, M. Healey, W. Kimmerer, P.B. Moyle, D. Murphy, D. Patten, S. Railsback, D. Reed, R. Spies, and R. Twiss. 2008. Prioritizing river restoration: projecting cumulative benefits of multiple projects: an example from the Sacramento-San Joaquin River System in California. *Environmental Management* 42:933–945.
- Krueper, D.J. 1993. Effects of land use practices on western riparian ecosystems. Pages 321–330 in D. Finch and P. Stangel (editors). *Status and Management of Neotropical Migratory Birds*. General Technical Report RM-229. U.S. Department of Agriculture, Forest Service, Rocky Mountain Range and Experiment Station, Fort Collins, Colorado. 422 p.
- Krueper, D.J., J. Bart, and T.D. Rich. 2003. Response of vegetation and breeding birds to the removal of cattle on the San Pedro River, Arizona. *Conservation Biology* 17:607–615.
- Jarvi, S.I., J.J. Schultz, and C.T. Atkinson. 2002. PCR diagnostics underestimate the prevalence of avian malaria (*Plasmodium relictum*) in experimentally-infected passerines. *The Journal of Parasitology* 88:153–159.
- Lima, S.L. 1998. Nonlethal effects in the ecology of predator-prey interactions. *BioScience* 48:25–34.
- _____. 2009. Predators and the breeding bird: behavioral and reproductive flexibility under the risk of predation. *Biological Reviews of the Cambridge Philosophical Society* 84:485–513.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- MacArthur, R.H. and J.W. MacArthur. 1961. On bird species diversity. *Ecology* 42:594–598.
- Marshall, R.M. and S.H. Stoleson. 2000. Threats, Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. U.S. Department of Agriculture, Forest Service General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah. pp. 13–24.
- Martin, T.E. 2011. The cost of fear. *Science* 334:3353–3354. December 9, 2011.
- Mason, J.T. 2015. The impact of anthropogenic noise on northern saw-whet owl (*Aegolius acadicus*) hunting behavior. Boise State University theses and dissertations. Paper 892.
<http://scholarworks.boisestate.edu/td/892>
- McDonald, D.B. and H. Caswell. 1993. Matrix methods for avian demography. Pages 139–185 in D.M. Power (editor). *Current Ornithology*. Plenum Press, New York, New York.
- McLeod, M.A. and A.R. Pellegrini. 2013. Southwestern Willow Flycatcher Surveys, Demography, and Ecology Along the Lower Colorado River and Tributaries, 2008–2012. Summary report submitted to the Bureau of Reclamation, Boulder City, Nevada, by SWCA Environmental Consultants, Flagstaff, Arizona.
- _____. 2014. Southwestern Willow Flycatcher Surveys, Demography, and Ecology Along the Lower Colorado River and Tributaries, 2013 Annual Report. Submitted to Bureau of Reclamation, Boulder City, Nevada, by SWCA Environmental Consultants, Flagstaff, Arizona.
- McLeod, M.A., T.J. Koronkiewicz, B.T. Brown, W.J. Langeberg, and S.W. Carothers. 2008a. Southwestern Willow Flycatcher Surveys, Demography, and Ecology Along the Lower Colorado River and Tributaries, 2003–2007. Five-year summary report submitted to the Bureau of Reclamation, Boulder City, Nevada, by SWCA Environmental Consultants, Flagstaff, Arizona.
- McLeod, M.A., T.J. Koronkiewicz, S.R. Nichols, B.T. Brown, and S.W. Carothers. 2008b. Southwestern Willow Flycatcher Surveys, Demography, and Ecology Along the Lower Colorado River and Tributaries, 2007 Annual Report. Submitted to Bureau of Reclamation, Boulder City, Nevada, by SWCA Environmental Consultants, Flagstaff, Arizona.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- McNeil, S.E., D. Tracy, J.R. Stanek, and J.E. Stanek. 2013. Yellow-billed Cuckoo Distribution, Abundance, and Habitat Use on the Lower Colorado River and its Tributaries. 2008-2012 Summary Report. U.S. Department of the Interior, Bureau of Reclamation, Lower Colorado Regional Office, Boulder City, Nevada.
- Moore, D. 2007. Vegetation Quantification of Southwestern Willow Flycatcher Nest Sites. Rio Grande from La Joya to Elephant Butte Reservoir Delta, New Mexico – 2004–2006. Bureau of Reclamation, Albuquerque, New Mexico.
- Moore, D. and D. Ahlers. 2006. 2006 Southwestern willow flycatcher study results: selected sites along the Rio Grande from Velarde to Elephant Butte Reservoir, New Mexico. Bureau of Reclamation, Fisheries and Wildlife Resources, Denver, Colorado.
- Morishita, T.Y., P.P. Aye, E.C. Ley, and B.S. Harr. 1999. Survey of pathogens and blood parasites in free-living passerines. *Avian Diseases* 43:549–552.
- Nilsson, C. and M. Svedmark. 2002. Basic principles and ecological consequences of changing water regimes: riparian plant communities. *Environmental Management* 30:468–480.
- Noon, B.R. and M. Farnsworth. 2000. Demographic Analysis of the Southwestern Willow Flycatcher: Kern River Population. Colorado State University. Report to the Bureau of Reclamation, Phoenix, Arizona.
- Palinauskas, V., G. Valkiūnas, C.V. Bolshakov, and S. Bensch. 2008. *Plasmodium relictum* (lineage P-SGS1): effects on experimentally infected passerine birds. *Experimental Parasitology* 120:372–80.
- Paradzick, C.E. 2005. Southwestern Willow Flycatcher Habitat Selection Along the Gila and Lower San Pedro Rivers, Arizona: Vegetation and Hydrogeomorphic Considerations. Arizona State University, Tempe, Arizona.
- Paxton, E.H., M.K. Sogge, S.L. Durst, T.C. Theimer, and J.R. Hatten. 2007. The Ecology of the Southwestern Willow Flycatcher in Central Arizona: A 10-Year Synthesis Report. U.S. Geological Survey Open-File Report 2007-1381. Reston, Virginia.
- Paxton, E.H., T.C. Theimer, and M.K. Sogge. 2011. Tamarisk biocontrol using tamarisk beetles: potential consequences for riparian birds in the southwestern United States. *The Condor* 113:255–265.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Peterson, D., A.R. Pellegrini, M.A. McLeod, and T.C. Theimer. 2015. Distance to standing water is negatively correlated with invertebrate biomass, nestling feeding rate, and productivity in southwestern willow flycatchers (*Empidonax traillii extimus*) in The Colorado Plateau VI: Science and Management at the Landscape Scale (pp. 262–270). University of Arizona Press.
- Robinson, R.A., B. Lawson, M.P. Toms, K.M. Peck, J.K. Kirkwood, J. Chantrey, I.R. Clatworthy, A.D. Evans, L.A. Hughes, O.C. Hutchinson, S.K. John, T.W. Pennycott, M.W. Perkins, P.S. Rowley, V.R. Simpson, K.M. Tyler, and A.A. Cunningham. 2010. Emerging infectious disease leads to rapid population declines of common British birds. *PloS One* 5:e12215.
- Rosenberg, K.V. 1991. *Birds of the Lower Colorado River Valley*. University of Arizona Press, Tucson, Arizona.
- Rosenfeld, J. 2003. Assessing the Habitat Requirements of Stream Fishes: An Overview and Evaluation of Different Approaches. *Transactions of the American Fisheries Society* 132: 953–968.
- Rosenfeld, J.S. and T. Hatfield. 2006. Information needs for assessing critical habitat of freshwater fish. *Canadian Journal of Fisheries and Aquatic Sciences* 63:683–698. DOI:10.1139/F05-242.
- Rudnicki, M., U. Silins, and V.J. Lieffers. 2004. Crown cover is correlated with relative density, tree slenderness, and tree height in lodgepole pine. *Forest Science* 50:356–363.
- Salt River Project. 2014. Southwestern willow flycatcher and yellow-billed cuckoo surveys at the Rockhouse Demonstration Site, River, Gila County, Arizona. 2014 Summary Report. Environmental Services Department, Siting and Studies, Phoenix, Arizona.
- Schlossberg, S.R. and M.P. Ward. 2004. Using conspecific attraction to conserve endangered birds. *Endangered Species Update* 21:132–138.
- Schmidt, K.A., J. Goheen, R. Naumann, R.S. Ostfeld, E.M. Schaubert, and A. Berkowitz. 2001. Experimental removals of strong and weak predators: mice and chipmunks preying on songbird nests. *Ecology* 82: 2927–2936.
- Schmidt, K.A., L.C. Nelis, N. Briggs, and R.S. Ostfeld. 2005. Invasive shrubs and songbird nesting success: effects of climate variability and predator abundance. *Ecological Applications* 15:258–265.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Sedgwick, J.A., editor. 2000. Willow Flycatcher (*Empidonax traillii*). Cornell Lab of Ornithology. Retrieved from The Birds of North America Online: Ithaca, New York.
<http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/533>
- Smith, D.M., J.F. Kelly, and D.M. Finch. 2006. Cicada emergence in southwestern riparian forest: influences of wildfire and vegetation composition. *Ecological Applications* 16:1608–1618.
- Sogge, M.K. 2000. Breeding season ecology. Chapter 6 (pages 57–70) in D.M. Finch and S.H. Stoleson (editors). *Status, Ecology, and Conservation of the Southwestern Willow Flycatcher*. General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Sogge, M.K., R.M. Marshall, S.J. Sferra, and T.J. Tibbitts. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. Technical Report NPS/NAUCPRS/NRTR-97/12. U.S. Department of the Interior, National Park Service, Colorado Plateau Research Station at Northern Arizona University.
- Sogge, M.K., S.J. Sferra, and E.H. Paxton. 2008. Tamarix as habitat for birds: implications for riparian restoration in the southwestern United States. *Restoration Ecology* 16(1):146–154.
doi: 10.1111/j.1526-100X.2008.00357.x
- Sogge, M.K., D. Ahlers, and S.J. Sferra. 2010. A Natural History Summary and Survey Protocol for the Southwestern Willow Flycatcher. U.S. Geological Survey Techniques and Methods 2A-10. Reston, Virginia.
- Stoleson, S.H., M.J. Whitfield, and M.K. Sogge. 2000. Demographic characteristics and population modeling. Chapter 8 (pages 83–94) in D.M. Finch and S.H. Stoleson (editors). *Status, Ecology, and Conservation of the Southwestern Willow Flycatcher*. General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Tamarisk Coalition. 2009. Colorado River Basin Tamarisk and Russian Olive Assessment. December 2009. Grand Junction, Colorado.
- Theimer, T., D. Peterson, A. Pellegrini, M.A. McLeod, and T. Koronkiewicz. 2011. Real and Artificial Nest Predation and Parental Nest Attendance Along the Lower Colorado River and Southern Nevada. U.S. Department of the Interior, Bureau of Reclamation, Lower Colorado Regional Office, Boulder City, Nevada.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

- Thompson, III, F.R. 2007. Factors affecting nest predation on forest songbirds in North America. *Ibis* 149(Suppl.2):98–109.
- Tucson Audubon. 2012. Arizona's Important Bird Areas.
http://www.tucsonaudubon.org/iba/IBA_Booklet_06-2012_in%20numerical%20order.pdf
- Unitt, P. 1987. *Empidonax traillii extimus*: an endangered subspecies. *Western Birds* 18(3):137–162.
- U.S. Fish and Wildlife Service (USFWS). 2002a. Southwestern Willow Flycatcher Recovery Plan, Albuquerque, New Mexico. U.S. Fish and Wildlife Service, Albuquerque, New Mexico.
- _____. 2002b. Southwestern Willow Flycatcher Recovery Plan, Appendix G: Management of Livestock Grazing in the Recovery of the Southwestern Willow Flycatcher. Albuquerque, New Mexico.
- _____. 2013. Designation of critical habitat for southwestern willow flycatcher; final rule. *Federal Register* 78(2):344-534.
- Vega Rivera, J.H., W.J. McShea, J.H. Rappole, and S.J. Hackett. 2003. Comparison of breeding and postbreeding movements and habitat requirements for the scarlet tanager (*Piranga olivacea*) in Virginia. *The Auk* 120:632–644.
- Ward, M.P. and S. Schlossberg. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18:519–525.
- Ware, H.E., C.J.W. McClure, J.D. Carlisle, and J.R. Barber. 2015. A phantom road experiment reveals traffic noise is an invisible source of habitat degradation. *Proceedings of the National Academy of Sciences* 112:12105–12109.
- Whitfield, M.J. and M.K. Sogge. 1999. Range-wide impact of brown-headed cowbird parasitism on the southwestern willow flycatcher (*Empidonax traillii extimus*). *Studies in Avian Biology* 18:182–190.
- Wiens, J.A., N.C. Stenseth, B. Van Horne, and R.A. Ims. 1993. Ecological mechanisms and landscape ecology. *Oikos*:369–380.
- Wiesenborn, W.D. and S.L. Heydon. 2007. Diets of breeding southwestern willow flycatchers in different habitats. *The Wilson Journal of Ornithology* 119:547–557.

**Southwestern Willow Flycatcher (*Empidonax traillii extimus*) (SWFL)
Basic Conceptual Ecological Model for the Lower Colorado River**

Wildhaber, M.L. 2011. Identifying structural elements needed for development of a predictive life-history model for pallid and shovelnose sturgeons. *Journal of Applied Ichthyology* 27:462–469.

Wildhaber, M.L., A.J. DeLonay, D.M. Papoulias, D.L. Galat, R.B. Jacobson, D.G. Simpkins, P.J. Baaten, C.E. Korschgen, and M.J. Mac. 2007. A conceptual life-history model for pallid and shovelnose sturgeons. U.S. Geological Survey, Circular 1315. Reston, Virginia.

ACKNOWLEDGMENTS

The authors would like to acknowledge Chris Dodge biologists with Reclamation, LCR MSCP; Carrie Ronning, Wildlife Group Manager , LCR MSCP; and Sonja Kokos, Adaptive Management Group Manager, LCR MSCP, who provided invaluable technical feedback and guidance during the development of the model process and production of this report. We would also like to acknowledge John Swett, Program Manager, LCR MSCP, for his leadership and support of this modeling effort that will guide and inform the work of the LCR MSCP well into the future.

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, 2011), Kondolf et al. (2008), and Burke et al. (2009) 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.

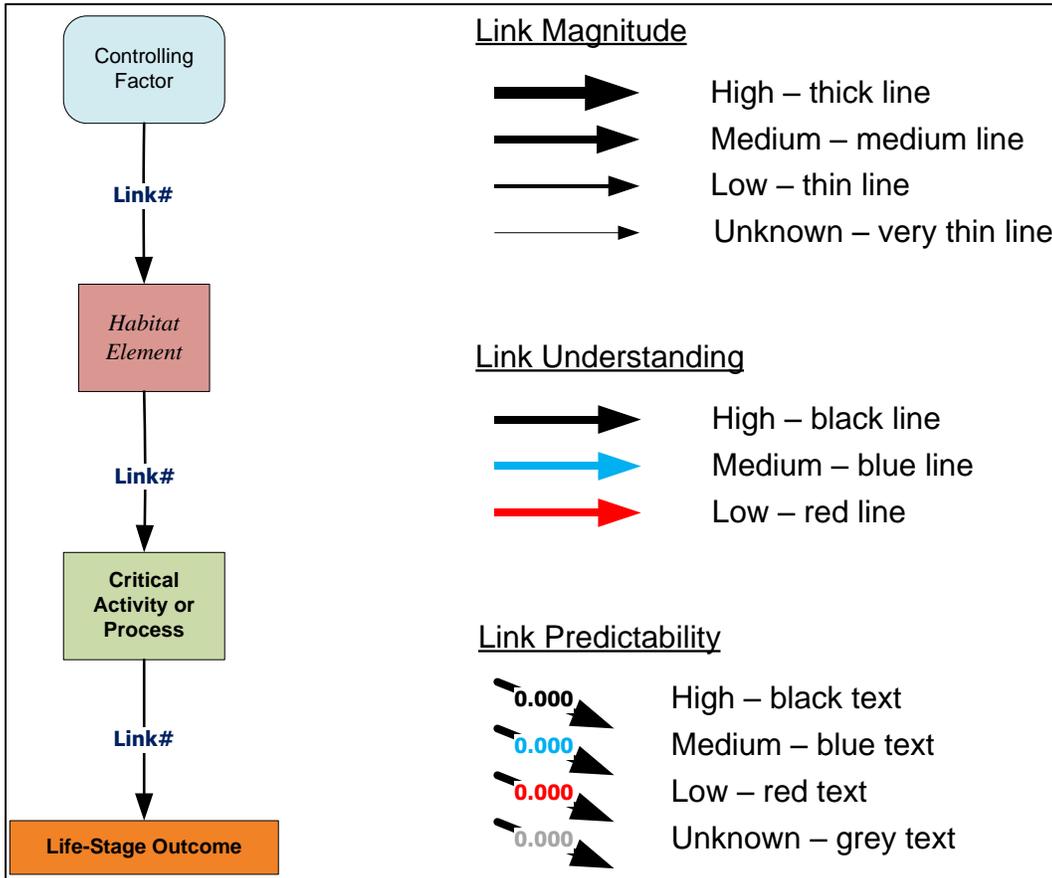


Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

LITERATURE CITED

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

ATTACHMENT 2

Southwestern Willow Flycatcher Habitat Data

Table 2-1.—Southwestern willow flycatcher habitat data

Habitat element	Range	Location	Citation
Canopy closure (over nest)	94%	Lower Colorado River	McLeod and Pellegrini 2013
	92.30%	Lower Colorado River	McLeod et al. 2007
	88.00%	Gila, Lower San Pedro	Paradzick 2005
	95.10%	Roosevelt Lake	Ellis et al. 2008
	91.5%, 92.4%, 93.8%	Virgin River, Utah	Dobbs et al. 2012
	93%	Kern River, California	Whitfield and Enos 1996 <i>in</i> Craig and Williams 1998
	89–97% coyote willow (<i>Salix exigua</i>) or Goodding's willow (<i>Salix gooddingii</i>) – recommended	Lower Colorado River	McLeod and Pellegrini 2013
	88.6%, 92.4%	Ash Valley, Pahrangat Valley Wildlife Management Areas, Nevada	Klinger and Furtek 2008
Community type	Mostly willow species, some tamarisk (<i>Tamarix</i> spp.) (shrubs and trees)	Middle Rio Grande, New Mexico	Moore 2007
	71% nests in box elder (<i>Acer negundo</i>)	Gila River, Arizona	Skaggs 1996 <i>in</i> Sogge 2000
	Goodding's willow and tamarisk	Lower Colorado River	Paradzick 2005
	Mix of native and exotic vegetation	Virgin River, Utah	Dobbs et al. 2012
	Most nests in tamarisk. Goodding's willow and Fremont cottonwood (<i>Populus fremontii</i>) present.	Gila River, Coolidge Dam – South Butte, Arizona	Graber et al. 2012
	Fremont cottonwood, Goodding's willow, and dense coyote willow understory – planted	Rockhouse, Salt River, Arizona	Salt River Project 2014
Distance to occupied patch	30–40 kilometers	Central Arizona	Paxton et al. 2007
	Up to 75 kilometers	Lower Colorado River	McLeod and Pellegrini 2013

Table 2-1.—Southwestern willow flycatcher habitat data

Habitat element	Range	Location	Citation
Humidity	2,019 Pascals mean diurnal vapor pressure; 1,866.6 Pascals mean nocturnal vapor pressure	Lower Colorado River	McLeod and Pellegrini 2013
Intermediate structure (density of understory layer)	Dense, no number provided	Lower Colorado River	Sogge et al. 2010
	3.64 shrub stems/ square meter – Dense vegetation in mid-canopy between 3–6 meters (m) in height	Middle Rio Grande, New Mexico	Moore 2007
	502.1 shrub stems/5-m plot, < 8-centimeter diameter at breast height	Virgin River, Utah	Dobbs et al. 2012
Linear width of patch	≥ 10 m	Lower Colorado River	Sogge et al. 2010; Sogge and Marshall 2000
Local hydrology (distance to water)	Within 10 m at beginning of season for > 50% sites; most average distances ≤ 20 m	Lower Colorado River	McLeod and Pellegrini 2013
	Mean distance 21.6 m	Elephant Butte Reservoir Delta, New Mexico	Moore 2007
	93% nests within 100 m of water; 87% sites within 50 m of surface water	Elephant Butte Reservoir, New Mexico	Moore and Ahlers 2006
	Most sites < 1m from water (farthest 198 m but in old river channel)	Lower Colorado River	Paradzick 2005
	3.3 m	Virgin River, Utah	Dobbs et al. 2012
	Mean monthly stream flow > 300 cubic feet. Higher and more consistent annual streamflow and previous year's flow between April – June is linked to a greater number of SWFL territories.	Gila River, Arizona	Graber et al. 2012

Table 2-1.—Southwestern willow flycatcher habitat data

Habitat element	Range	Location	Citation
Local hydrology (distance to water) (continued)	SWFL nested close to water's edge, moving territories accordingly in response to water levels fluctuating year to year. 2004 – 187.6 ± 4.9 m (pre-inundation); 2006 – 3.5 ± 3.0 m (post-inundation)	Roosevelt Lake	Ellis et al. 2008
Patch size	0.01–70 hectares (ha)	Lower Colorado River	U.S. Fish and Wildlife Service 2013
	4,000 square meters – 1.72 ha	Lower Colorado River	Sedgewick 2000
	0.8 ha – several hundred hectares	Lower Colorado River	Sogge et al. 2010
	0.6 ha	Grand Canyon	Sogge et al. 1997
	100 ha	Lake Mead	McKernan 1997
	2.0–25.5 ha	Virgin River, Utah	Dobbs et al. 2012
Temperature	40.4 degrees Celsius mean maximum; 20.9 degrees Celsius mean minimum	Lower Colorado River	McLeod and Pellegrini 2013
Tree density	High densities of small/medium stems	Lower Colorado River	McLeod and Pellegrini 2013
	500–1,300 stems/ha young trees	Lower Colorado River	Paradzick 2005
	8,349.1 ± 246 2.5–8 centimeter diameter at breast height stems/ha	Lower Colorado River	McLeod et al. 2007
	2,829 stems/ha – tree stem density greater in nest plots than random plots	Middle Rio Grande, New Mexico	Moore 2007

Note: The data presented in this table reflect those available in the literature at the time this model was developed. These data have not been validated.

There are other habitat elements that are important to the SWFL model. These include anthropogenic disturbance, brood size, conspecific attraction, diversity of vegetation, food availability, genetic diversity and infectious agents, matrix community, nest predator and cowbird density, predator density, and previous year's use. They are not included in the table because there has been no specific data collected about them. In addition, they may be challenging elements for which to develop precise land management direction.

LITERATURE CITED

- Craig, D. and P.L. Williams. 1998. Willow Flycatcher (*Empidonax traillii*) in The Riparian Bird Conservation Plan: A Strategy for Reversing the Decline of Riparian-Associated Birds in California. California Partners in Flight.
- Dobbs, R.C., M. Huizinga, C.N. Edwards, and R.A. Fridell. 2012. Status, Reproductive Success, and Habitat Use of Southwestern Willow Flycatchers on the Virgin River, Utah, 2008–2011. Publication Number 12-36. Utah Division of Wildlife Resources, Salt Lake City.
- Ellis, L.A., D.M. Weddle, S.D. Stump, H.C. English, and A.E. Graber. 2008. Southwestern Willow Flycatcher Final Survey and Nest Monitoring Report 2008, Research Technical Guidance Bulletin. Arizona Game and Fish Department, Phoenix.
- Graber, A.E., T.J. Koronkiewicz, and J.L. Granger. 2012. Southwestern Willow Flycatcher Surveys and Nest Monitoring Along the Gila River Between Coolidge Dam and South Butte, 2011. Annual summary report submitted to the Bureau of Reclamation, Glendale, Arizona. Flagstaff, Arizona: SWCA Environmental Consultants.
- Klinger, C. and B. Furtek. 2008. Southwestern Willow Flycatcher and Yellow-billed Cuckoo Survey and Monitoring at Select Sites in Southern Nevada, 2007 Annual Report. Nevada Department of Wildlife, Wildlife Diversity Program, Job Progress Report.
- McKernan, R.L. 1997. Status, Distribution, and Habitat Affinities of the Southwestern Willow Flycatcher Along the Lower Colorado River: Year 1 – 1996. Report prepared for the Bureau of Reclamation, Lower Colorado River Region, Boulder City, Nevada. 42 p.
- McLeod, M.A., T. J. Koronkiewicz, B.T. Brown, and S.W. Carothers. 2007. Southwestern Willow Flycatcher Surveys, Demography, and Ecology Along the Lower Colorado River and Tributaries, 2006. Bureau of Reclamation, Lower Colorado River Multi-Species Conservation Program, Boulder City, Nevada.
- McLeod, M.A. and A.R. Pellegrini. 2013. Southwestern Willow Flycatcher Surveys, Demography, and Ecology Along the Lower Colorado River and Tributaries, 2008–2012. Bureau of Reclamation, Lower Colorado River Multi-Species Conservation Program, Boulder City, Nevada.

- Moore, D. 2007. Vegetation Quantification of Southwestern Willow Flycatcher Nest Sites. Rio Grande from La Joya to Elephant Butte Reservoir Delta, New Mexico – 2004–2006. Bureau of Reclamation, Albuquerque, New Mexico.
- Moore, D. and D. Ahlers. 2006. 2006 Southwestern Willow Flycatcher Study Results: Selected Sites Along the Rio Grande from Velarde to Elephant Butte Reservoir, New Mexico. Bureau of Reclamation, Fisheries and Wildlife Resources, Denver, Colorado.
- Paradzick, C.E. 2005. Southwestern Willow Flycatcher Habitat Selection Along the Gila and Lower San Pedro Rivers, Arizona: Vegetation and Hydrogeomorphic Considerations. Arizona State University, Tempe.
- Paxton, E.H., M.K. Sogge, S.L. Durst, T.C. Theimer, and J.R. Hatten. 2007. The Ecology of the Southwestern Willow Flycatcher in Central Arizona: A 10-Year Synthesis Report. U.S. Geological Survey, Reston, Virginia.
- Salt River Project. 2014. Southwestern Willow Flycatcher and Yellow-billed Cuckoo Surveys at the Rockhouse Demonstration Site, Salt River, Gila County, Arizona, 2014 Summary Report. Environmental Services Department, Siting and Studies, Phoenix, Arizona.
- Sedgwick, J.A. 2000. Willow flycatcher (*Empidonax traillii*). Cornell Lab of Ornithology. Retrieved from the Birds of North America Online: Ithaca, New York.
<http://bna.birds.cornell.edu.bnaproxy.birds.cornell.edu/bna/species/533>
- Sogge, M.K. and R.M. Marshall. 2000. A survey of current breeding habitats. Chapter 5 (pages 43–56) in D.M. Finch and S.H. Stoleson (editors). Status, Ecology, and Conservation of the Southwestern Willow Flycatcher. General Technical Report RMRS-GTR-60. U.S. Department of Agriculture, Forest Service, Rocky Mountain Research Station, Ogden, Utah.
- Sogge, M.K., R.M. Marshall, S.J. Sferra, and T.J. Tibbitts. 1997. A Southwestern Willow Flycatcher Natural History Summary and Survey Protocol. Technical Report NPS/NAUCPRS/NRTR-97/12. U.S. Department of the Interior, National Park Service, Colorado Plateau Research Station at Northern Arizona University.
- Sogge, M.K., D. Ahlers, and S.J. Sferra. 2010. A Natural History Summary and Survey Protocol for the Southwestern Willow Flycatcher. U.S. Department of the Interior, U.S. Geological Survey, Reston, Virginia.