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

Life Stages, Critical Biological Activities and Processes, Habitat Elements, and Controlling Factors

Photos courtesy of the Bureau of Reclamation.

December 2013

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Lower Colorado River Multi-Species Conservation Program

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Life Stages, Critical Biological Activities and Processes, Habitat Elements, and Controlling Factors

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

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ACRONYMS AND ABBREVIATIONS

CEM	conceptual ecological model
ERP	Sacramento-San Joaquin Delta Ecosystem Restoration Program
km	kilometer(s)
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
Reclamation	Bureau of Reclamation
SWFL	southwestern willow flycatcher

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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 habitat and species restoration, and the methods used to measure SWFL habitat and population conditions. This document is provided to describe and support the interactive model for SWFL provided to Reclamation as a package of Microsoft Visio diagrams and a Microsoft Excel Workbook.

Conceptual Ecological Models

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

The CEM applied to the 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 shape the abundance, distribution, and persistence of the species in that area.

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

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

  Critical biological activities and processes – These consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage.

- **Habitat elements** – These consist of the specific habitat conditions that are necessary or sufficient for the critical activities and processes to take place or that interfere with critical activities or processes. The abundance and distribution of habitat elements control the rates (intensities) of the activities and processes that they affect.

- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distribution, and quality of important habitat elements. Controlling factors are also called "drivers."

The CEM identifies the causal relationships among these components that affect the rate at which individuals of a species survive and transition (recruit) from one life stage to the next. Further, the model 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 status (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.

Structure of the SWFL Conceptual Ecological Model

The SWFL conceptual ecological model addresses the SWFL population along the river and lakes of the lower Colorado River (LCR) and in wildlife refuges and other protected areas along the LCR managed as SWFL habitat under the auspices of the LCR MSCP Habitat Conservation Plan. The model thus addresses the landscape as a whole rather than any single reach or managed area.

The basic sources of the information on the CEM summarized below include McLeod and Pellegrini (2013), Paxton et al. (2007), Sogge et al. (2010), Finch et al. (2002), Reclamation (2004, 2008), and BIO-WEST (2005). These publications summarize and cite large bodies of earlier studies. The model also integrates numerous additional sources, particularly reports and articles completed since these publications; information on current research projects; and the expert knowledge of LCR MSCP biologists. Our purpose is not to simply provide an updated literature review but to integrate the available information into a CEM.

The SWFL conceptual ecological model distinguishes and assesses four life stages as follows:

1. Egg
2. Nestling
3. Juvenile
4. Breeding adult

The SWFL conceptual ecological model distinguishes 9 critical biological activities or processes relevant to 1 or more of 4 life stages, 21 habitat elements relevant to 1 or more of these 9 critical biological activities or processes for 1 or more life stages, and 8 controlling factors that affect 1 or more of these 21 habitat elements. Because the LCR and its refuges comprise 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, molt, nest site selection, foraging, nest attendance, predation, temperature regulation, predation and brood parasitism, and eating.

The 21 habitat elements identified across all life stages are: canopy cover, understory density, patch size, linear width of patch, food availability, community type, matrix community, local hydrology, tree density, parent nest attendance, temperature, humidity, predator and cowbird density, siblings, brood size, genetic diversity and infectious agents, anthropogenic disturbance, previous year's use, distance to occupied patch, and diversity of vegetation.

The eight controlling factors identified across all habitat elements are: pesticide application, main stem water storage-delivery management, fire management, grazing, mechanical thinning, natural thinning, planting regime, and nuisance species introduction and management.

INTRODUCTION

This document presents the core components of 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 actions aimed at habitat and species restoration, and the methods used to measure SWFL habitat and population conditions. The CEM methodology used here follows that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012) with modifications.

The model addresses the SWFL population along the river and lakes of the lower Colorado River (LCR) and in wildlife refuges and other protected areas along the LCR managed as SWFL habitat under the auspices of the LCR MSCP Habitat Conservation Plan. The model thus addresses the landscape as a whole rather than any single reach or managed area.

The basic sources of the information on the CEM summarized below include McLeod and Pellegrini (2013), Paxton et al. (2007), Sogge et al. (2010), Finch et al. (2002), Reclamation (2004, 2008), and BIO-WEST (2005). These publications summarize and cite large bodies of earlier studies. The model also integrates numerous additional sources, particularly reports and articles completed since these publications; information on current research projects; and the expert knowledge of LCR MSCP biologists. Our purpose is not to simply provide an updated literature review, but to integrate the available information into a CEM.

Conceptual Ecological Model Purposes

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

Conceptual ecological models explicitly identify: (1) the parameters or attributes that best characterize resource conditions; (2) the physical and ecological 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 these factors affect 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 we expect the characteristics of the resource to 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 see others as less so. Through the CEM, scientists and managers can identify which hypotheses – and the assumptions on which they rest – 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 and clarify the CEM, improving certainty about some aspects of the model while requiring changes to others. These changes then guide the next cycle of management action and research. The CEM, through its successive iterations, becomes the record for increasing knowledge and the ability to manage the system.

Conceptual Ecological Model Structure for the SWFL

The CEM methodology used for the SWFL 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 Kondolf et al. (2008) and Burke et al. (2009) to provide greater detail on causal linkages and outcomes. Attachment A provides a detailed description of the methodology. The model is a “life history” model, as is common for CEMs focused on individual species (Wildhaber et al. 2007), and it distinguishes the major life stages or events through which the individuals of a species must pass in order to complete a full reproductive cycle. It then identifies the factors that shape the likelihood that, within the study area, individuals in each life stage will survive to the next stage. These factors are key to maintaining the abundance, distribution, and persistence of the species in the study area.

The CEM has four core components, as explained in attachment A:

- **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 reproductive cycle.

- **Critical biological activities and processes** – These consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage. Examples of activities and processes for a bird species may include nesting, foraging, avoiding predators, and avoiding other specific hazards. Activities and processes may be considered "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 that are necessary or sufficient for the critical activities and processes to take place or that interfere with critical activities or processes. The abundance and distribution of habitat elements control the rates (intensities) of the activities and processes that they affect. Taken together, the suite of habitat elements for a life stage is called the "habitat template" for that life stage. Defining the habitat template also may involve estimating specific thresholds or ranges of suitable values for particular habitat elements, outside of which one or more critical life activities or processes begin to fail – if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics – including human actions – that determine the abundance, spatial and temporal distribution, and quality 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 breeding territories may depend on factors such as river flow rates and flow-path morphology, which in turn may depend on factors such as watershed geology, vegetation, and climate.

The CEM both characterizes these four components and identifies the causal relationships among them that affect the rate at which individuals of a species survive and transition (recruit) from one life stage to the next. Further, the model assesses each causal link 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 rate of success of the life stage, support or limit the rate of each critical biological activity or process, and support or limit the quality of each habitat element (as it affects other habitat elements, or affects 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 A 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.

SWFL LIFE STAGE MODEL

A life stage consists of a 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. The last two parts of this definition – concerning habitats and ecological interactions – are the most crucial for the purposes of the present CEM for the LCR MSCP.

SWFL Life Stage 1 – Egg

We consider the egg stage to be the first in the life cycle of the SWFL. It begins when the egg is laid and ends at hatching. 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).

SWFL Life Stage 2 – Nestling

The nestling stage lasts from the time the egg hatches until fledging. 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).

SWFL Life Stage 3 – 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 2005; Reclamation 2008).

SWFL Life Stage 4 – Breeding Adult

The adult stage begins when the bird returns to the breeding grounds after its first winter and ends when it departs the breeding grounds during fall migration. Generally, adults arrive on the breeding grounds between early May and early June with after-second-year males arriving earlier—setting up territories before females arrive (Sedgwick 2000; BIO-WEST 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).

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 but provide good conditions for 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 four life stages as follows and as shown on figure 1. The life stages are numbered sequentially beginning with the gametes and eggs.

1. Egg
2. Nestling
3. Juvenile
4. Breeding adult

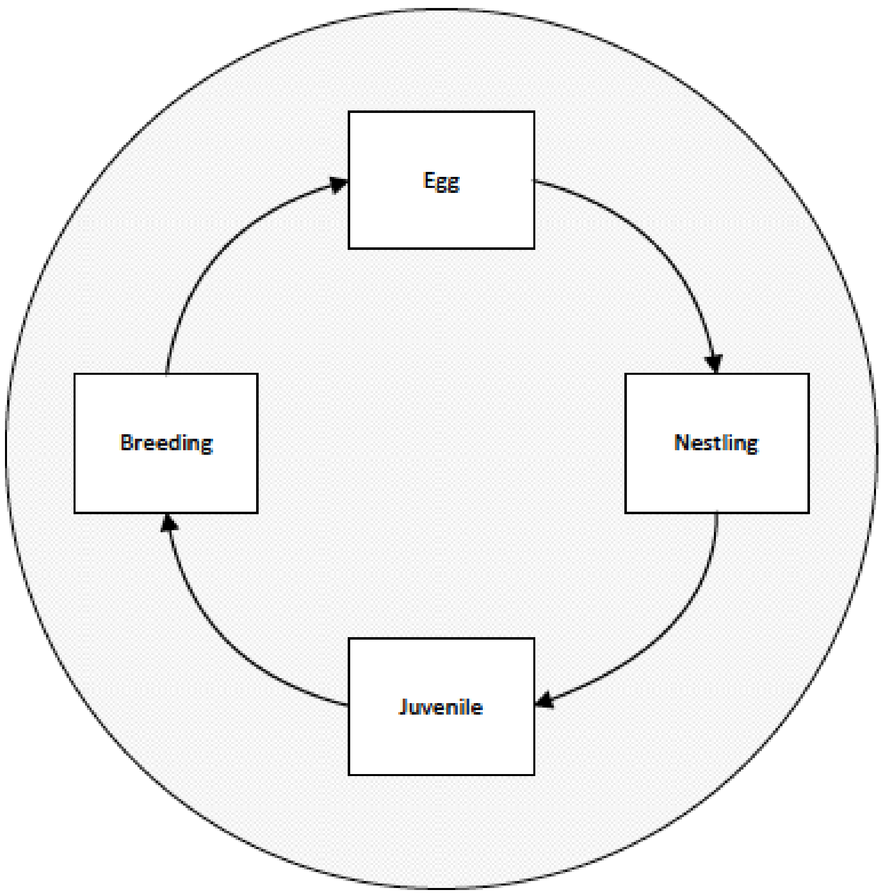

Figure 1.—Proposed CEM for the SWFL.

CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES

Critical biological activities and processes consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage. Critical activities and processes may be considered critical “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).

This section identifies a set of nine critical activities and processes that affect one or more SWFL life stages. Some of these activities or processes differ in their details between life stages. However, using the same labels for the same *kinds* of activities or processes across all life stages makes comparison and integration of the CEMs for the individual life stages across the entire life cycle less difficult. Table 1 lists the nine critical activities and processes and their distribution across life stages.

Table 1.—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 ➔ 🡻 Critical biological activity or process	**Egg**	**Nestling**	**Juvenile – Breeding grounds**	**Adult – Breeding**
Disease	X	X	X	X
Molt		X		
Nest site selection				X
Foraging			X	X
Nest attendance				X
Predation			X	X
Temperature regulation	X	X	X	X
Predation and brood parasitism	X	X		
Eating		X		

Disease

This process refers to diseases caused either by lack of genetic diversity or by infectious agents. 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). All life stages are conceivably susceptible to disease.

Molt

Nestling SWFL must molt from natal down into juvenile plumage. Molting is an energetically costly process that may make nestlings more susceptible to death when resources are scarce.

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).

Foraging

SWFL are hawking insectivores that forage above the canopy, along edges, and within forest openings (Finch et al. 2002; Reclamation 2004). 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.

Nest Attendance

The female does most of the incubating and brooding, but the male helps with feeding of the young (Sedgwick 2000). Breeding adults attend the nest, and this affects the survival of nestlings and eggs.

Predation

Predation is a threat in all life stages, and it obviously affects survival. The predators of and rates of predation upon eggs and nestlings are much better understood (Theimer et al. 2011) than predation upon adults (Finch et al. 2002).

Temperature Regulation

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

Predation and Brood Parasitism

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

Eating

This process only applies to the nestling stage because they must eat to stay alive and develop, but do not actively forage within their environment in the same way as the juveniles and adults. A nestling's ability to eat is determined by the foraging and provisioning rate of its parents. Some elements such as siblings, brood size, and genetic diversity are not traditionally considered aspects of habitat, but are included in this section because of their effects on critical biological activities and processes.

HABITAT ELEMENTS

As noted earlier, habitat elements consist of specific, pivotal habitat conditions that ensure, allow, or interfere with critical activities and processes.

This section identifies 21 habitat elements that affect 1 or more critical biological activities or processes across the four SWFL life stages. Some of these habitat elements apply to multiple spatial scales. For example, canopy cover could act at the patch and microhabitat scales, with SWFL choosing patches with the preferred amount of open areas for foraging and nest sites within those patches with enough canopy cover to regulate nest temperature. 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. Table 2 lists the 21 habitat elements and their distribution across the four SWFL life stages.

Table 2.—Distribution of SWFL habitat elements among life stages

Life stage ➔ ➔ Critical activity or process	**Egg**	**Nestling**	**Juvenile – Breeding grounds**	**Adult – Breeding**
Canopy cover	X	X	X	X
Understory density	X	X	X	X
Patch size	X	X	X	X
Linear width of patch	X	X	X	X
Food availability	X	X	X	X
Community type	X	X	X	X
Matrix community	X	X	X	X
Local hydrology	X	X	X	X
Tree density	X	X	X	X
Parent nest attendance	X	X		
Temperature	X	X	X	X
Humidity	X	X	X	X
Predator and cowbird density	X	X		
Predator density			X	X
Siblings		X	X	
Brood size				X
Genetic diversity and infectious agents	X	X	X	X
Anthropogenic disturbance	X	X	X	X
Previous year's use				X
Distance to occupied patch				X
Diversity of vegetation				X

The diagrams and other mentions of habitat elements elsewhere in this document identify the habitat elements by a short name of mostly one or two words such as "predator density." However, each name in fact refers to some variant of a longer phrase such as "abundance and distribution of predators." The definitions below document this full name and meaning.

Canopy Cover

Defined as: **The density of foliage in the overstory.** This element refers to the percent canopy closure of canopy vegetation in the vicinity of the SWFL nest site. Canopy cover 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 thermal regulation (Rosenberg 1991; but see Balluff 2012), and camouflage from nest predators, although heterogeneity in canopy cover within a given patch or landscape may also be desirable (see the “Diversity of Vegetation” section below). Canopy cover 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).

Understory Density

Defined as: **The density of the understory layer.** This element refers to the visual density of vegetation (i.e., concealment) below the uppermost canopy layer. Dense understory vegetation is a common characteristic of SWFL nesting habitat (Paxton et al. 2007; McLeod and Pellegrini 2013). A more dense understory may support a more diverse and abundant invertebrate food supply as well as provide protection or concealment from predators.

Patch Size

Defined as: **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), patch size affects the number of breeding pairs that an area can support as well as the density of predators, competitors, and brood parasites.

Linear Width of Patch

Defined as: **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.

Food Availability

Defined as: **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 nestling and juvenile stages. However, SWFL tend to be generalist insectivores (Wiesenborn and Heydon 2007) and therefore may be able to adapt their diet to a variety of conditions—lessening the effect of food availability on SWFL populations. Although eggs obviously do not eat, food availability still affects the foraging behavior and success of brooding adults and therefore indirectly affects the survival of an egg.

Community Type

Defined as: **The abundance and distribution of habitat with a suitable species composition.** 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 broadleaf deciduous habitats at different elevations (McLeod and Pellegrini 2013). They also have been shown to nest successfully in areas dominated by exotic species such as tamarix (Paxton et al. 2007).

Matrix Community

Defined as: **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. For example, adjacent agricultural landscapes may have elevated pesticide loads, which may affect foraging by adult and juvenile birds.

Local Hydrology

Defined as: **Aspects such as the distance to standing water or the presence of adjacent water bodies as well as the 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. Flycatchers are riparian obligates (Sogge et al. 2010), which are typically found within 10 meters of water at the beginning of the nesting season

(McLeod and Pellegrini 2013). Therefore, the timing of certain hydrological events such as flooding is important for site selection. The presence of moist soil or standing water affects food availability (supporting more invertebrates etc.) and may provide cooler temperatures and more humid conditions that are necessary for egg and chick survival in these desert systems (McLeod and Pellegrini 2013).

Tree Density

Defined as: **The stem density of trees.** This element refers to the number of trees per acre. The greater the tree and/or shrub density, the greater the likelihood of denser vegetative cover. Further, SWFL may use the number of stems as a criterion for site selection (McLeod and Pellegrini 2013).

Parent Nest Attendance

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

Temperature

Defined as: **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). Thermal regulation is necessary for survival of chicks and adults, and flycatchers nest in areas with moderated temperature ranges (McLeod et al. 2008). 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).

Humidity

Defined as: **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 is sites with higher humidity (McLeod et al. 2008).

Predator and Cowbird Density

Defined as: **The abundance and distribution of 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 egg or nestling life stages 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 whether predator activity may vary in relation to other factors (e.g., time of day, patch size and width, matrix community type, etc.).

Predator Density

Defined as: **The abundance and distribution of predators that affect SWFL during post-fledgling and adult stages.** This element refers to a set of closely related variables that affect the likelihood that different kinds of predators will encounter and successfully prey on 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 whether predator activity may vary in relation to other factors (e.g., time of day, patch size and width, matrix community type, etc.).

Siblings

Defined as: **The presence of siblings in the nest.** This element refers to the number of siblings in the nest or that fledge, requiring ongoing parental care. The greater the number of young, the less food may be available for each, potentially affecting growth and survival of individual chicks.

Brood Size

Defined as: **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 as well as other factors such as predator density (see "Predator and Cowbird Density").

Genetic Diversity and Infectious Agents

Defined as: **The genetic diversity of SWFL individuals and the types, abundance, and distribution of infectious agents.** 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. 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, and parasites that individual SWFL are likely to encounter during each life stage.

Anthropogenic Disturbance

Defined as: **Human activity within or surrounding a given habitat patch, including noise, pollution, and other disturbances associated with human activity.** An anthropogenic disturbance such as noise (reviewed by Barber et al. 2010; Francis and Barber 2013), and even non-consumptive human activity, can have negative effects on wildlife (reviewed by Boyle and Samson 1985).

Previous Year's Use

Defined as: **The location of the previous year's breeding attempt and whether or not it 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 the next year (Paxton et al. 2007).

Distance to Occupied Patch

Defined as: **The linear distance of a given patch of riparian forest to the nearest occupied patch.** Movement of SWFL between patches of riparian habitat is most likely within 30–40 kilometers (km) in central Arizona (Paxton et al. 2007) and less than 75 km 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

Defined as: **Either horizontal or vertical diversity of the vegetation structure at the patch or microhabitat scales or diversity of community types 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 sites with dense shrub and canopy cover, which likely have high foliage height diversity. Horizontal diversity – or variation in vegetation density within a patch – also has been shown to positively affect site use by SWFL (Hatten and Paradzick 2003; Paxton et al. 2007).

CONTROLLING FACTORS

As noted in the "Introduction," controlling factors consist of environmental conditions and dynamics – both natural and anthropogenic – that determine the abundance, spatial and temporal distribution, and quality of the conditions that comprise the habitat template. A hierarchy of such factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on more immediate controlling factors that are within the scope of potential human manipulation.

The 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.

Pesticide Application

This factor addresses pesticide applications that may occur on or adjacent to riparian habitat of the LCR region. Effects may include sublethal poisoning of SWFL via ingestion of treated insects, pollution of runoff into wetland habitats that are toxic to prey of the SWFL, and a reduced invertebrate food supply.

Main Stem Water Storage-Delivery Management

The LCR consists of a chain of reservoirs separated by flowing reaches. 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. The dynamic nature of a free-flowing river creates a mosaic of riparian habitats, and thus, a natural flow regime may be beneficial to the SWFL. Flycatchers also will use habitat patches adjacent to reservoirs that change with rising and falling water levels (Paxton et al. 2007).

Fire Management

This factor addresses any fire management (whether prescribed or suppression) that may occur along the LCR 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 a species that pose threats to SWFL 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 (Finch et al. 2002).

Grazing

This factor addresses the grazing activity on riparian habitats along the LCR that could affect SWFL or their habitat. Grazing may thin the understory or even prevent the establishment of cottonwood and willow seedlings (Kauffman et al. 1997).

Mechanical Thinning

This factor addresses the active removal of vegetation from areas within the LCR region. Effects may include creation of habitat that supports or excludes SWFL or support of species that pose threats to SWFL as predators, competitors, or carriers of infectious agents. This factor includes the thinning of vegetation within both riparian and matrix communities.

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.

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, patch size).

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. The 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 canopy or shrub cover. For example, although flycatchers may successfully nest in sites dominated by invasive salt cedar (*Tamarix* spp.), salt cedar may negatively affect habitat in other ways (e.g., by lowering the water table) (Di Tomaso 1998). Any control measures to remove salt cedar-dominated habitat used for nesting by flycatchers need to include rapid replacement with other dense vegetation (Paxton et al. 2007).

The complicated nature of the relationship between Tamarix and SWFL is highlighted by another introduced species—the Tamarix beetle (*Diorhabda carinulata*). The Tamarix beetle was introduced to the LCR region in order to control invasive tamarix (Bateman et al. 2013; McLeod and Pellegrini 2013). However, defoliation of tamarix due to beetle infestation causes increases in temperature and decreases in humidity (Bateman et al. 2013), thereby degrading areas dominated by tamarix as habitat for SWFL (McLeod and Pellegrini 2013).

CONCEPTUAL ECOLOGICAL MODEL BY LIFE STAGE

The following four sections summarize the CEM for each 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 activities and processes, the controlling factors that determine the abundance and quality of these habitat elements, and the causal links among them. The model sections specifically refer to wildlife refuges and other protected areas managed as SWFL habitat and thus addresses this landscape as a whole rather than any single reach or managed area.

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

- **Character and direction** categorizes a causal relationship as positive, negative, involving a threshold response, or complex. Positive means that an increase (or decrease) in the causal agent results in an increase (or decrease) in the affected element, and negative means that an increase (or decrease) in the agent results in a decrease (or increase) in the affected element. Thus, positive or negative here do *not* mean that a relationship is beneficial or detrimental. The terms only provide information analogous to the sign of a correlation coefficient. Threshold means that change in the causal agent must cross some value before we see an effect. Complex means that there is more going on than a simple positive, negative, or threshold effect.

- **Magnitude** refers to "…the degree to which a linkage controls the outcome relative to other drivers. While the models are designed to encompass critical drivers, linkages, and outcomes, this concept recognizes that some are more important than others in determining how the system works" (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.

- **Predictability** refers to the consistency with which the causal agent shapes the affected condition. The more variable the relationship, or the more the relationship depends on the interactions and effects of other factors, the less predictable the relationship (DiGennaro et al. 2012).

- **Scientific 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.

The CEM for each life stage thus identifies the causal relationships that most strongly support or limit the rate of success of the life stage, support or limit the rate of each critical biological activity or process, and support or limit the quality of each habitat element (as it affects other habitat elements or affects critical biological activities or processes).

The diagrams for the life stages use a common set of conventions for identifying the controlling factors, habitat elements, critical biological activities and processes, and life stage success. Figure 2 illustrates these conventions. The diagrams also use a common set of conventions for displaying information about the causal links. Figure 2 also illustrates these latter conventions. The full methodology involves the assessment of the above four properties for each causal link; however, displaying the information on character and predictability results in extremely confusing diagrams. For this reason, the model diagrams for the individual life stages only display information on the magnitude and scientific understanding of each causal link. A separate spreadsheet tool records the assessment of all four properties for each causal link along with the underlying rationale and citations. The CEM diagrams for the four life stages follow.

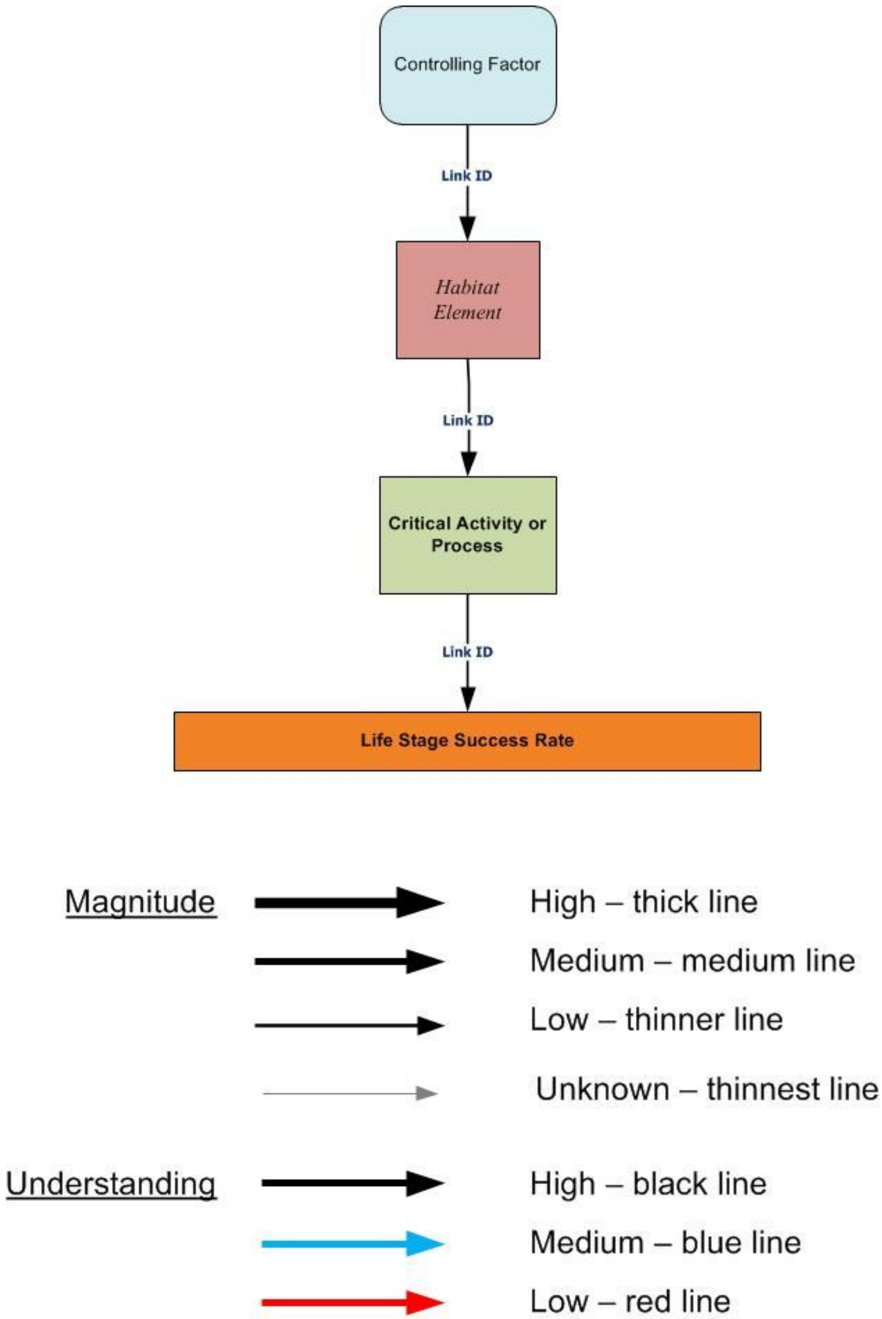

Figure 2.—Diagram conventions for LCR MSCP conceptual ecological models.

The causal relationships between controlling factors and habitat elements are essentially the same across all four life stages. For this reason, this section reserves the discussion of controlling factor-habitat element linkages to a separate section, covering all four life stages together.

SWFL Life Stage 1 – Egg

We consider the egg stage to be the first in the life cycle of the SWFL. It begins when the egg is laid and ends at hatching. Success during this life stage – successful transition to the next stage – involves egg survival, maturation, and hatching. Since the eggs do not actively interact with their environment, critical biological activities and processes consist only of critical processes, which include:

1. **Temperature regulation** – The embryo must maintain an optimum temperature to develop within the egg.

   The CEM recognizes humidity and temperature as primary habitat elements directly affecting temperature regulation. Secondary habitat elements include local hydrology, parent nest attendance, understory density, canopy cover, , and tree density.

2. **Predation and brood parasitism** – Both predation and brood parasitism affect the survival of an egg 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 predation and brood parasitism into one process for this stage.

   The CEM recognizes community type, linear width of patch, parent nest attendance, patch size, understory density, predator and cowbird density, canopy cover, anthropogenic disturbance, and tree density as secondary habitat elements affecting predation and brood parasitism.

3. **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 secondary habitat elements affecting disease.

Southwestern Willow Flycatcher (*Empidonax traillii extimus*)
Basic Conceptual Ecological Model

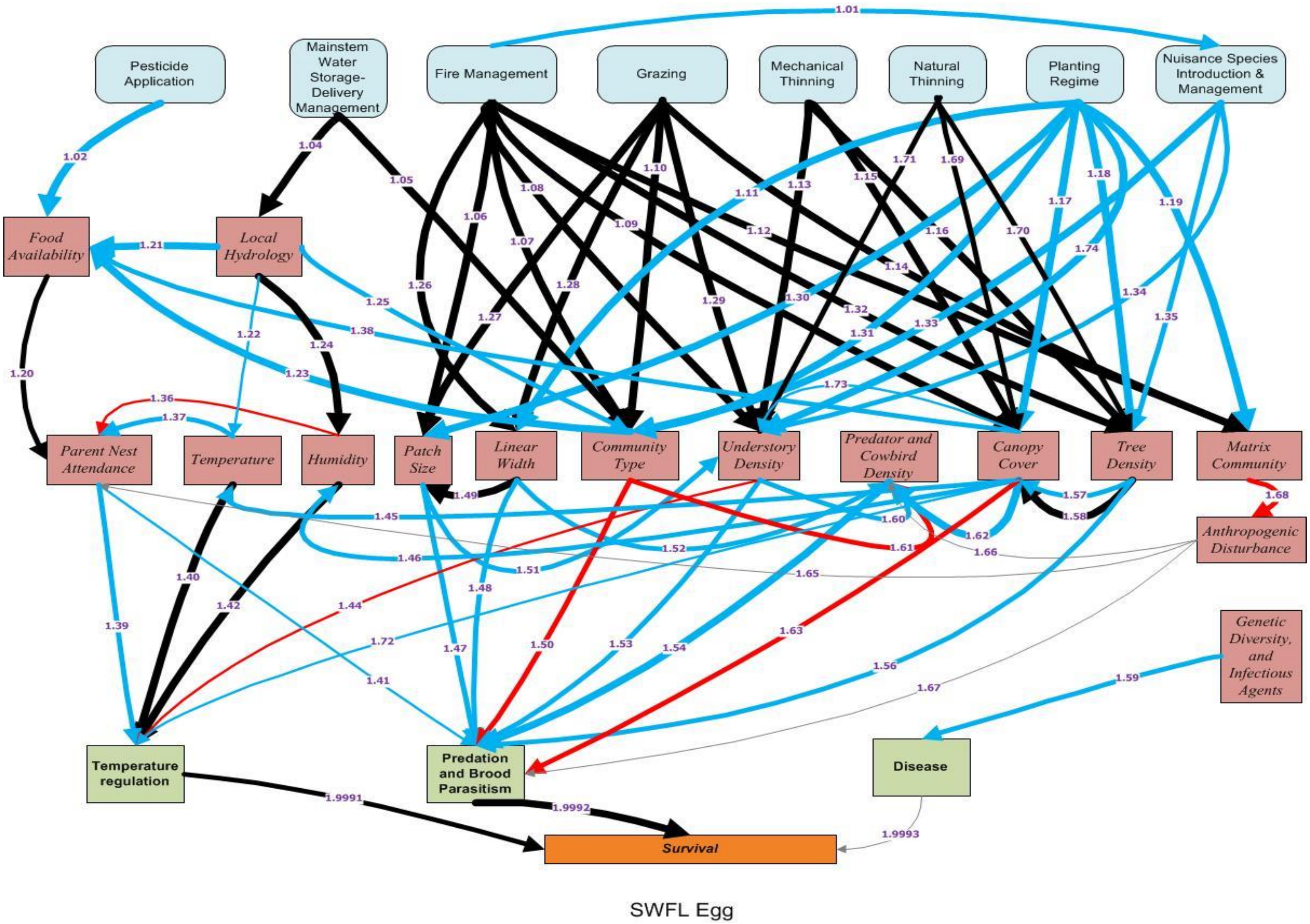

Figure 3.—Basic CEM diagram for life stage 1 – egg.

SWFL Life Stage 2 – Nestling

The nestling stage lasts from the time the egg hatches until fledging. Success during this life stage – successful transition to the next stage –involves organism survival, maturation, molt, and fledging. The organisms actively interact with their environment. Critical biological activities and processes therefore consist of both activities and processes, which include:

1. **Temperature regulation** – The nestling must maintain an optimum temperature to develop and survive.

   The CEM recognizes humidity as the primary habitat element directly affecting temperature regulation. Secondary habitat elements affecting temperature regulation include parent nest attendance, canopy cover, temperature, and understory density.

2. **Predation and brood parasitism** – Both predation and brood parasitism affect the survival of a nestling 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 predation and brood parasitism into one process for this stage.

   The CEM recognizes community type, linear width of patch, parent nest attendance, patch size, understory density, predator and cowbird density, canopy cover, anthropogenic disturbance, and tree density as secondary habitat elements affecting predation and brood parasitism.

3. **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 secondary habitat element affecting disease.

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

   The CEM recognizes parent nest attendance, siblings, and anthropogenic disturbance as secondary habitat elements affecting eating.

5. **Molt** – The nestling must molt into juvenile plumage.

   The CEM does not recognize any habitat elements as directly affecting molt.

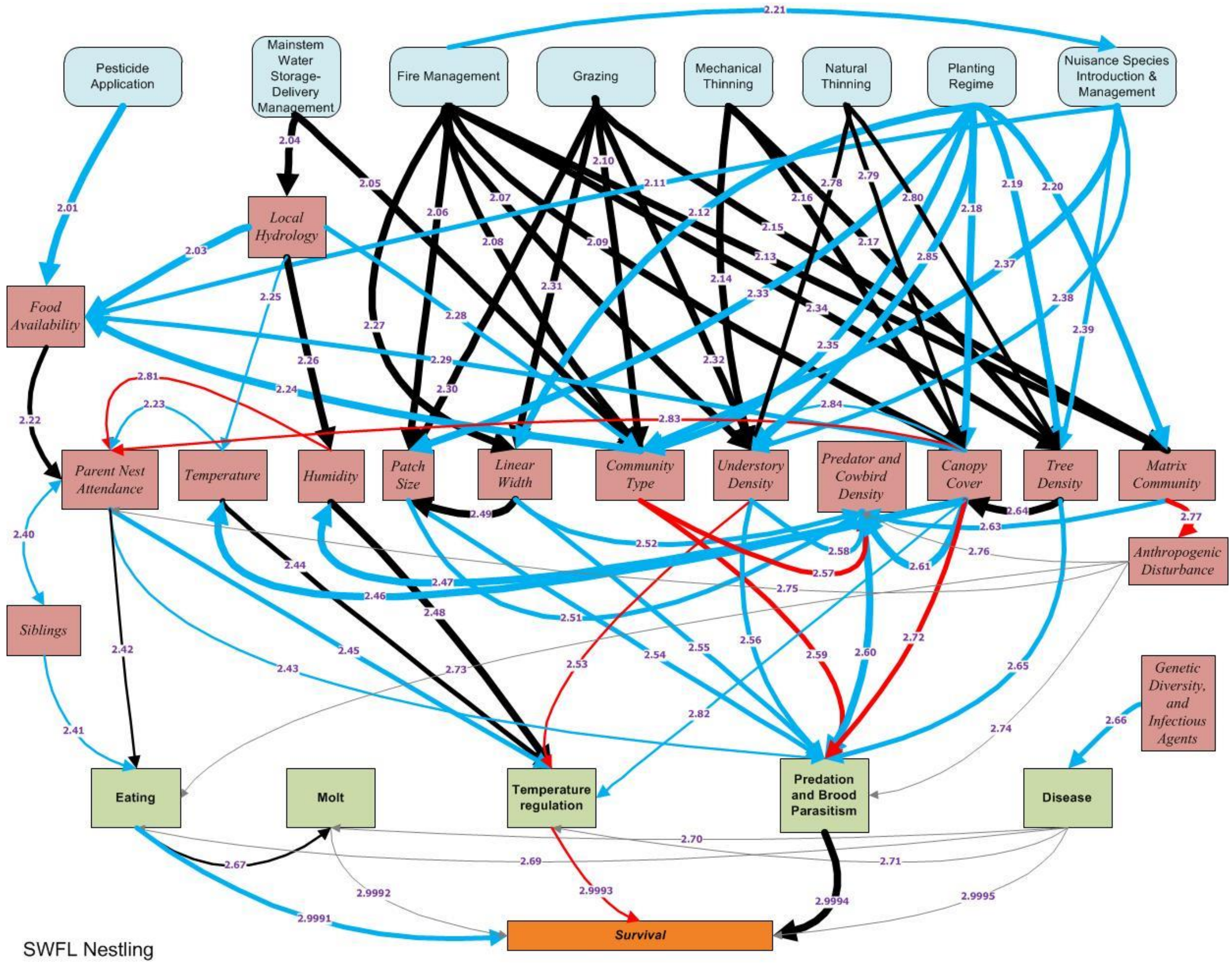

Figure 4.—Basic CEM diagram for life stage 2 – nestling.

SWFL Life Stage 3 – Juvenile

The juvenile stage begins at fledging and ends when the bird returns to the breeding grounds the next year. Success during this life stage – successful transition to the next stage –involves organism survival and maturation. The organisms actively interact with their environment. Critical biological activities and processes therefore again consist of both activities and processes, which include:

1. **Temperature regulation** – The juvenile must maintain an optimum temperature to survive.

   The CEM recognizes humidity as a primary habitat element directly affecting temperature regulation. Secondary habitat elements affecting temperature regulation include understory density and temperature.

2. **Predation** – Brood parasitism is no longer a threat to the survival of the bird and therefore is no longer included with predation.

   The CEM recognizes community type, linear width of patch, parent nest attendance, patch size, understory density, predator density, canopy cover, anthropogenic disturbance, and tree density as secondary habitat elements affecting predation.

3. **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 secondary habitat element affecting disease.

4. **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 CEM recognizes parent nest attendance, food availability, canopy cover, and anthropogenic disturbance as secondary habitat elements affecting foraging.

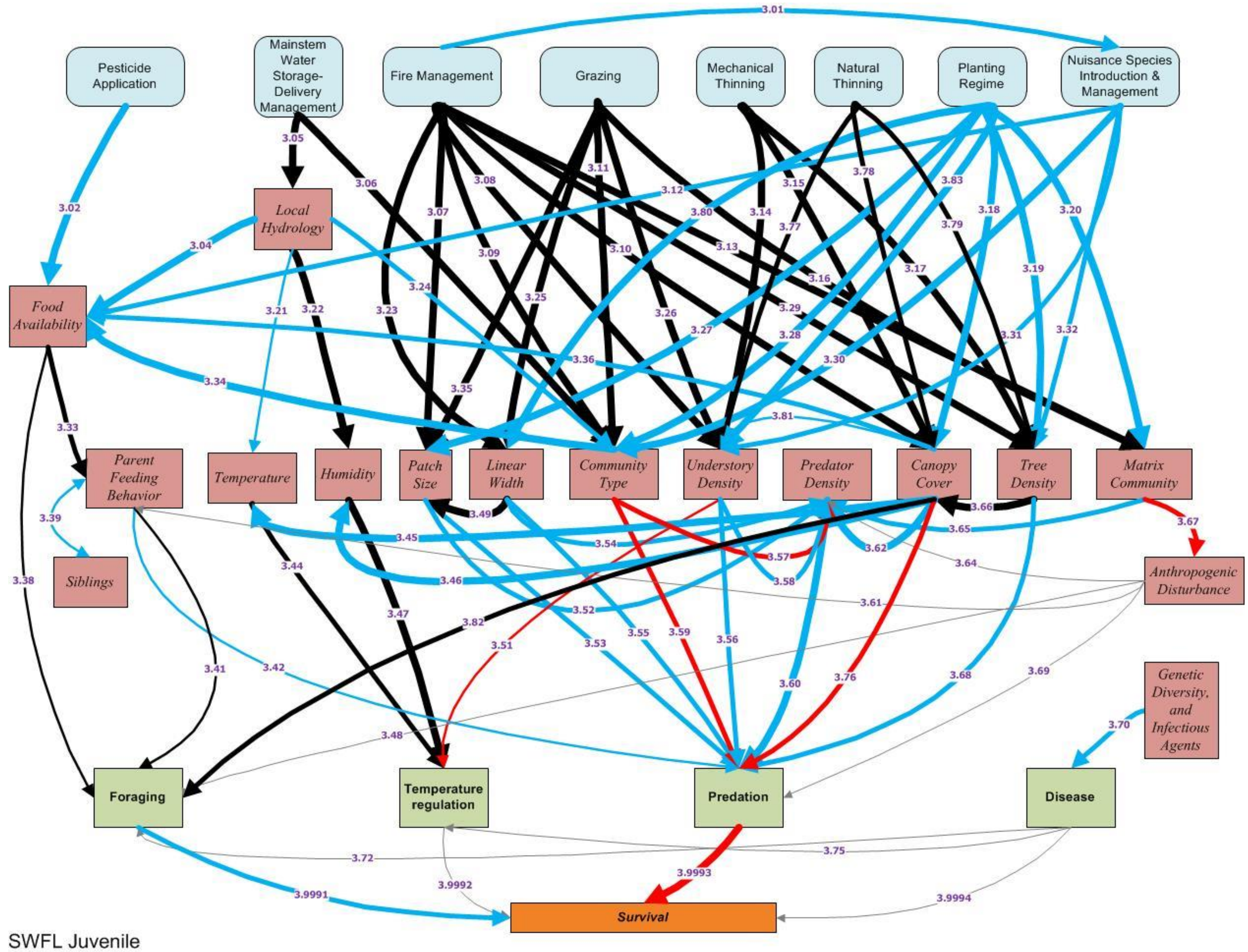

Figure 5.—Basic CEM diagram for life stage 3 – juvenile.

SWFL Life Stage 4 – Breeding Adult

The adult stage begins when the bird returns to the breeding grounds after its first winter and ends when it departs the breeding grounds during fall migration. 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. Floaters are most likely to be second-year males (Paxton et al. 2007). The organisms actively interact with their environment. Critical biological activities and processes therefore again consist of both activities and processes, which include:

1. **Temperature regulation** – The adult must maintain an optimum temperature to survive.

   The CEM recognizes humidity as the primary habitat element affecting temperature regulation. Secondary habitat elements affecting temperature regulation include temperature, canopy cover, and understory density.

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

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

3. **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 secondary habitat element affecting disease.

4. **Foraging** – The breeding adult must forage to feed itself and its young.

   The CEM recognizes community type and diversity of vegetation as primary habitat elements affecting foraging. Secondary habitat elements affecting foraging include brood size, food availability, canopy cover, matrix community, and anthropogenic disturbance.

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 humidity, diversity of vegetation, and community type as primary habitat elements affecting nest site selection. Secondary habitat elements affecting nest site selection include previous year's use, distance to occupied patch, canopy cover, understory density, linear width of patch, matrix community, patch size, predator density, canopy cover, temperature, anthropogenic disturbance, and tree density.

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

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

CAUSAL RELATIONSHIPS

The CEM diagrams show the causal relationships identified from the literature for each of the four SWFL life stages. The causal relationships extend from controlling factors to other controlling factors, from controlling factors to habitat elements, from habitat elements to other habitat elements, from habitat elements to critical biological activities and processes, and from critical biological activities and processes to other critical biological activities and processes. However, for ease of interpretation, the diagrams only represent a subset of the information contained in the model (i.e., the diagrams do not present the character and direction of each cause-effect relationship or the predictability [consistency] of the effect). The assessment is intended to help identify the causal relationships that have the greatest effect on the success (survivorship and recruitment outcome) of each life stage, based on the current state of knowledge, and the causal relationships about which the greatest uncertainty exists concerning their effects on survivorship and recruitment.

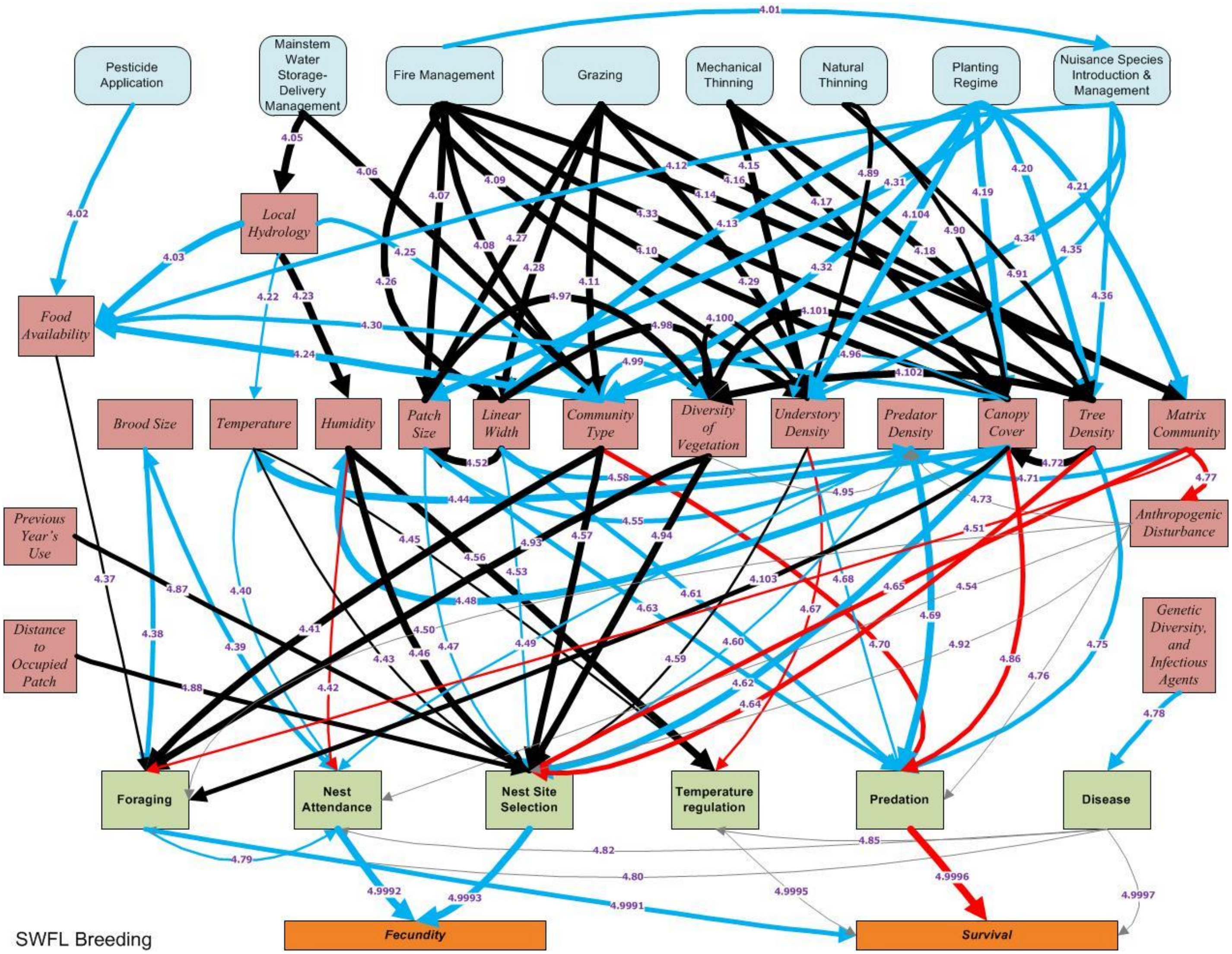

Figure 6.—Basic CEM diagram for life stage 4 – breeding adult.

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ATTACHMENT 1

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

Overview of Methodology for Building Conceptual Ecological Models

The conceptual ecological models (CEMs) for species covered by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) 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 the National Marine Fisheries Service. The Bureau of Reclamation participates in this program.

The ERP methodology for building CEMs incorporates common best practices for presenting these models for species covered by the LCR MSCP and identified in Habitat Conservation Plan (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 transitions from one stage/event to the next.

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

- It characterizes these interrelationships using a "*driver-linkage-outcomes*" approach. Linkages are cause-and-effect relationships between drivers and outcomes. Outcomes are the transition rates and their associated metrics (such as larval production or mortality).

- 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 status (certainty) of present scientific understanding of the effect. Below, we present the draft definitions for these four variables, after DiGennaro et al. (2012).

The LCR MSCP conceptual ecological models will expand this ERP methodology, incorporating the recommendations of Kondolf et al. (2008) and Burke et al. (2009) for a more hierarchical approach. This expanded approach provides greater detail on causal linkages and outcomes by dividing outcomes into two types: (1) activities and processes and (2) habitat elements. This expansion therefore calls for identifying **three** model components for each life stage or transition, and the causal linkages among them, as follows:

- **Critical biological activities and processes** – These consist of the activities in which the species must engage and the biological processes that must take place during each life stage to sustain an acceptable rate of transition (recruitment) to the next life stage. Examples of activities and processes include mating, foraging, avoiding predators, avoiding other specific hazards, egg maturation, and seed germination.

- **Habitat elements**– These consist of the specific habitat conditions that are necessary or sufficient for the critical activities and processes to take place or that interfere with critical activities or processes. Defining the full "template" of these elements for each life stage or transition also requires identifying habitat conditions that can interfere with these critical activities and processes. The abundance and distribution of habitat elements control the rates (intensities) of the activities and processes that they affect. Defining the habitat template also may involve estimating specific thresholds or ranges of suitable values for particular habitat elements, outside of which one or more critical life activities or processes begin to fail – if the state of the science supports such estimates.

- **Controlling factors** – These consist of environmental conditions and dynamics –including human actions – that determine the abundance, spatial and temporal distribution, and quality 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 breeding territories may depend on factors such as river flow rates and flow-path morphology, which in turn may depend on factors such as watershed geology, vegetation, and climate.

This expanded approach permits the consideration of five possible types of causal linkages on which management actions may focus for each life stage of a species: (1) from one controlling factor to another, (2) from controlling factors to elements of the habitat template, (3) from one element of the habitat template to another, (4) from elements of the habitat template to critical biological activities and processes, and (5) from one critical biological activity or process to others. Each controlling factor may affect more than one element of the habitat template, and each element of the habitat element may be affected by more than one controlling factor. Similarly, each habitat element may affect more than one biological activity or process, and each biological activity or process may be affected by more than one habitat element. 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 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.

Expanding the ERP methodology with this added level of detail will ensure that the CEMs explicitly identify the habitat conditions that support or impede the rates of success of each critical biological activity or process for each life stage and therefore the rate of recruitment from each life stage to the next. Such explicit consideration of habitat conditions is crucial for identifying critical monitoring and research questions and guiding habitat restoration for the species addressed by the LCR MSCP.

Conceptual Ecological Models as Hypotheses

The CEM for each species produced with this methodology will constitute a collection of hypotheses for that species. These hypotheses will concern: (1) the species' life history; (2) the species' habitat requirements and constraints; (3) the factors that control the abundance, spatial and temporal distribution, and quality of these habitat conditions; and (4) the causal relationships among these. Knowledge about these elements and relationships may vary, ranging from well settled to very tentative. Such variation in the degree of 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 these three CEMs will document the degree of certainty of current knowledge concerning each element of the model for each species as indicated in part by the degree of agreement/disagreement among the experts. In some cases, it will be possible also to represent differences in the interpretations or arguments offered by different experts in the form of alternative hypotheses. Categorizing the degree of agreement/disagreement concerning the elements of the CEM will help to more easily identify the topics of greatest uncertainty or controversy.

Documentation and Diagrams

The CEM for each species will include the definition and rationale for each of the following:

(1) Species life cycle, identifying all life stage/events and their transitions.

(2) The critical biological activities and processes for each life stage and transition.

(3) The critical habitat conditions that support or impede each critical biological activity or process.

(4) The controlling factors affecting the abundance, spatial and temporal distribution, and quality of the conditions that comprise the habitat template.

(5) The causal linkages among (2), from (3) to (2), among (3), from (4) to (3), and among (4).

The CEM will also include an assessment of each causal linkage based on the four variables noted above 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 spreadsheet and text will present the rationale for the assessment findings for each of these four variables. The definitions for these four variables will follow those of the ERP methodology.

The CEM for each species will include two types of diagrams: (1) a summary diagram of the species life cycle and the controlling factors affecting each stage and transition and (2) a more detailed diagram for individual life stages that shows the individual elements of the model for that stage (critical biological activities and processes, habitat elements, controlling factors) and their causal relationships. The more detailed diagrams will use many of the conventions of the ERP conceptual ecological models (Williams 2010; DiGennaro 2012), expanded as suggested by Kondolf et al. (2008) and Burke et al. (2009).

Methods for Characterizing Causal Relationships

The following information is adapted from DiGennaro et al. (2012). It incorporates the ERP methodology for assessing causal links among the four dimensions of: (1) the character and direction of the effect, (2) the importance of the effect, (3) the predictability (consistency) of the effect, and (4) the status (certainty) of present scientific understanding of the effect.

- **Character and direction** categorizes a causal relationship as positive, negative, or involving a threshold response. Positive means that an increase (or decrease) in the causal agent results in an increase (or decrease) in the affected element, and negative means that an increase (or decrease) in the agent results in a decrease (or increase) in the affected element.

- **Magnitude** refers to "…the degree to which a linkage controls the outcome relative to other drivers. While the models are designed to encompass critical drivers, linkages, and outcomes, this concept recognizes that some are more important than others in determining how the system works." 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. For purposes of the LCR MSCP conceptual ecological models, the score for magnitude will be calculated as the average of the scores for intensity, spatial scale, and temporal scale (tables 1–3).

- **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 is based on understanding of the driver, and the nature of how it is linked to the outcome, and thus captures variability. For example, understanding of processes may be high, but there may be natural variability either on an inter-annual and/or a seasonal basis that is unpredictable. Or the strength of relationships and the magnitude of effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult." Table 4 presents the scoring framework for predictability.

- **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 5 presents the scoring framework for understanding.

The ERP methodology applies a consistent approach to characterize these linkage attributes by rating magnitude, predictability, and understanding on a scale of high, medium, or low. The following tables provide the rating definitions for these four increments to assess linkage magnitude, predictability, and understanding.

Table 1.—Criteria for scoring the intensity of a cause-effect relationship, one of three variables averaged to produce the overall score for “magnitude” (after DiGennaro et al. 2012, Table 2)

Intensity – The strength of the effect, either positive or negative, on the population or habitat of a given species. Intensity takes into account the complete driver-linkage-outcome chain leading to the effect of interest.	
High	Expected major effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics at the places and times where the effect occurs.
Medium	Expected moderate effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics at the places and times where the effect occurs.
Low	Expected minor effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics at the places and times where the effect occurs.

Table 2.—Criteria for scoring the spatial scale of a cause-effect relationship (after DiGennaro et al. 2012, Table 1)

Spatial scale – The spatial scale of the effect on the population or habitat of a given species. Spatial scale takes into account the complete driver-linkage-outcome chain leading to the effect of interest.	
High	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics occurs at a large spatial scale – landscape or basin scale.
Medium	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics occurs at a moderate spatial scale – regional or reach scale.
Low	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics occurs at a small spatial scale – local or site scale.

Table 3.—Criteria for scoring the temporal scale of a cause-effect relationship (after DiGennaro et al. 2012, Table 1)

Temporal scale – The time scale of the effect on the population or habitat of a given species. Temporal scale takes into account the complete driver-linkage-outcome chain leading to the effect of interest.	
High	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics emerges, persists, or can be reversed only over a very long time scale – decades or longer.
Medium	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics emerges, persists, or can be reversed over a time scale of one or two decades.
Low	Effect on natural productivity, abundance, spatial distribution and/or diversity (both genetic and life history diversity), habitat quality, spatial configuration, and/or dynamics emerges, persists, or can be reversed over a time-scale of less than a decade.

Table 4.—Criteria for scoring the predictability of a cause-effect relationship (after DiGennaro et al. 2012, Table 3)

Predictability – The likelihood that a given causal agent will produce an effect of interest.	
High	Magnitude of effect is largely unconstrained by variability (i.e., predictable) in ecosystem dynamics or other external factors.
Medium	Magnitude of effect moderately depends on other highly variable ecosystem processes or uncertain external factors.
Low	Magnitude of effect greatly depends on other highly variable ecosystem processes or uncertain external factors.

Table 5.—Criteria for scoring the 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 and in scientific reasoning among experts familiar with the ecosystem.
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 or uncertainty in peer-reviewed studies from within the ecosystem of concern and in scientific reasoning among experts familiar with the ecosystem.