



# Lower Colorado River Multi-Species Conservation Program

*Balancing Resource Use and Conservation*

## MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW) Basic Conceptual Ecological Model for the Lower Colorado River

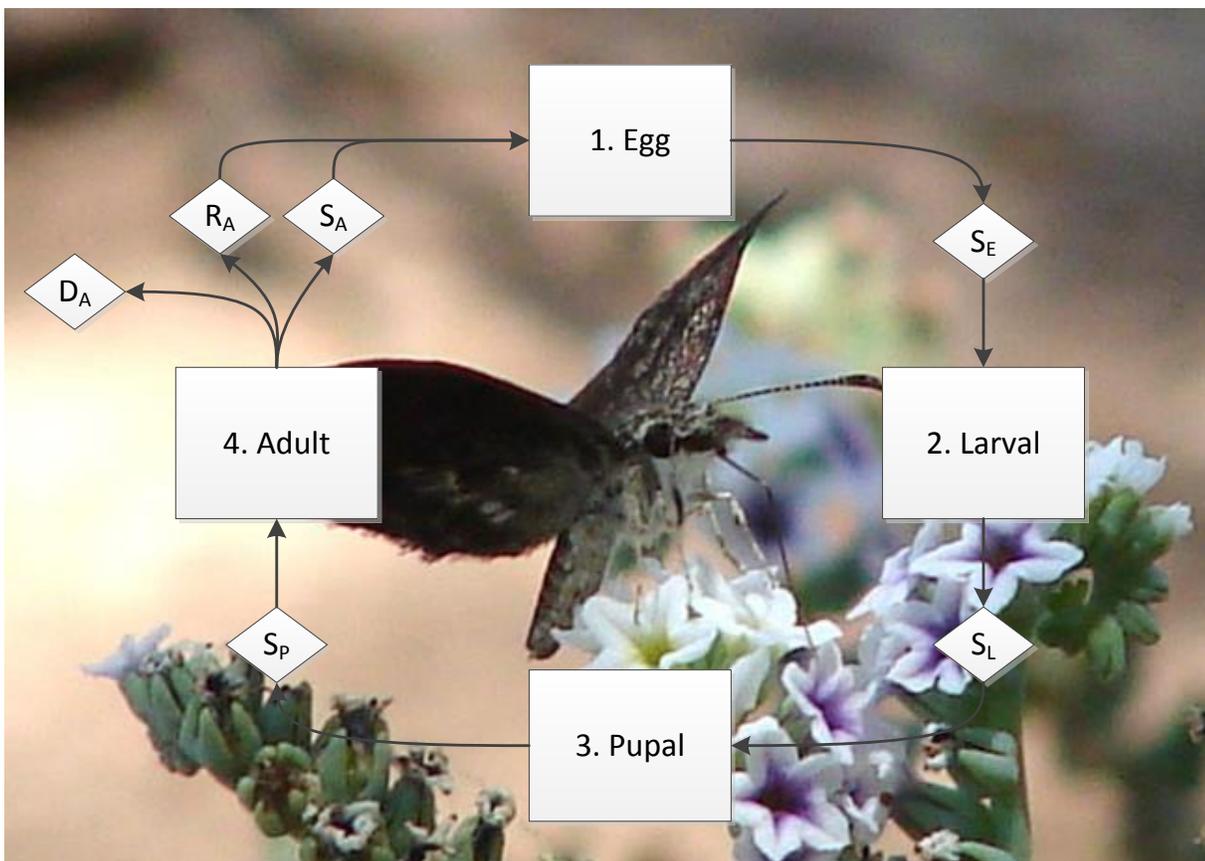


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October 2015

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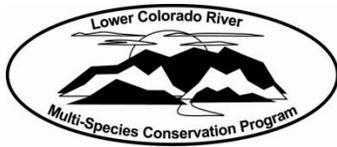
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The Nature Conservancy



# Lower Colorado River Multi-Species Conservation Program

## MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW) Basic Conceptual Ecological Model for the Lower Colorado River

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# ACRONYMS AND ABBREVIATIONS

CEM	conceptual ecological model
CVCA	Cibola Valley Conservation Area
eDNA	environmental deoxyribonucleic acid
EPA	United States Environmental Protection Agency
HCP	Habitat Conservation Plan
hr	hour(s)
km	kilometer(s)
km/hr	kilometer(s) per hour
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
m	meter(s)
mg	milligram(s)
mg/L	milligram(s) per liter
MNSW	MacNeill's sootywing skipper ( <i>Hesperopsis graciellae</i> )
mph	mile(s) per hour
Reclamation	Bureau of Reclamation

## Symbols

~	approximately
°C	degrees Celsius ( <i>aka</i> Centigrade)
>	greater than
≥	greater than or equal to
<	less than
±	plus or minus

## Definitions

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

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

**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.

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

**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.

# CONTENTS

	Page
<b>Foreword</b> .....	v
<b>Executive Summary</b> .....	<b>ES-1</b>
Conceptual Ecological Models .....	ES-1
Conceptual Ecological Model Structure .....	ES-2
Key Results .....	ES-4
<b>Chapter 1 – Introduction</b> .....	<b>1</b>
Conceptual Ecological Model Purposes .....	2
Conceptual Ecological Model Structure .....	3
<b>Chapter 2 – MNSW Life Stage Model</b> .....	<b>7</b>
Proposed Life Stages for MacNeill’s Sootywing Skipper .....	7
Egg Stage .....	7
Larval Stage .....	8
Pupal Stage.....	9
Adult Stage.....	9
<b>Chapter 3 – Critical Biological Activities and Processes</b> .....	<b>13</b>
Contamination and Infection.....	13
Feeding/Watering.....	15
Hiding/Resting .....	17
Mating .....	18
Ovipositing.....	19
Physiological Stress .....	20
Predation .....	21
<b>Chapter 4 – Habitat Elements</b> .....	<b>23</b>
Chemical Contaminants .....	24
Competitors.....	24
Fire Regime.....	25
Infectious Agents .....	26
Inundation Regime.....	26
Nectar Sources .....	27
Predators .....	28
Quailbush Litter Condition .....	30
Quailbush Patch Distribution.....	30
Quailbush Patch Size and Structure.....	31
Quailbush Shrub Condition.....	32
Scientific Study.....	33
Soil Moisture.....	34

	Page
Soil Salinity.....	35
Soil Nitrogen.....	35
<b>Chapter 5 – Controlling Factors.....</b>	<b>37</b>
Offsite Land Management and Use .....	38
Onsite Fire Management.....	39
Onsite Vegetation Management.....	39
Onsite Visitation and Study .....	39
Onsite Water Management .....	40
Reach-Scale Water Management.....	40
<b>Chapter 6 – Conceptual Ecological Model by Life Stage.....</b>	<b>41</b>
Methodology .....	41
Quailbush Ecology.....	44
MNSW Life Stage 1 – Egg Stage .....	48
MNSW Life Stage 2 – Larval Stage .....	55
MNSW Life Stage 3 – Pupal Stage.....	63
Nectar Source Ecology .....	69
MNSW Life Stage 4 – Adult Stage.....	73
<b>Chapter 7 – Causal Relationships Across All Life Stages.....</b>	<b>83</b>
Effects of Critical Biological Activities and Processes on Life-Stage Outcomes .....	83
Effects of Critical Biological Activities and Processes on Each Other .....	85
Effects of Habitat Elements on Critical Biological Activities and Processes.....	86
Effects of Habitat Elements on Each Other .....	89
Effects of Controlling Factors on Habitat Elements .....	93
Potentially Influential Causal Relationships with Low Understanding.....	95
<b>Chapter 8 – Discussion and Conclusions .....</b>	<b>99</b>
Literature Cited .....	103
Acknowledgments.....	109

## Tables

Table		Page
1	MNSW life stages and life-stage outcomes .....	7
2	MNSW critical biological activities and processes by life stage .....	13
3	MNSW nectar sources .....	15
4	MNSW habitat elements and the critical activities and processes they directly affect .....	23
5	Proportion of Lepidoptera in diets of insectivorous birds along the LCR valley, 1976–80, by season (after Anderson 2012) .....	29
6	MNSW controlling factors and the habitat elements they directly affect .....	37
7	Direct effects of critical biological activities and processes on life-stage outcomes (number of life stages in which relationship occurs) .....	84
8	Direct effects of critical biological activities and processes on other critical biological activities and processes (number of life stages in which relationship occurs) .....	85
9	Direct effects of habitat element on critical biological activities and processes (number of life stages in which relationship occurs) .....	87
10	Direct effects of habitat elements on other habitat elements (number of life stages in which relationship occurs) .....	90
11	Direct effects of controlling factors on habitat elements (number of life stages in which relationship occurs) .....	93
12	High-magnitude but poorly understood relationships between habitat elements and other variables (number of life stages in which relationship occurs) .....	95
13	High-magnitude but poorly understood relationships between habitat elements and other variables (number of life stages in which relationship occurs) .....	96
14	High-magnitude but poorly understood relationships between critical biological activities and processes and other variables (number of life stages in which relationship occurs) .....	97

## Figures

Figure		Page
1	Proposed MNSW life history model.....	11
2	Diagram conventions for LCR MSCP species CEMs. ....	43
3	Causal relationships affecting quailbush ecology across all MNSW life stages. ....	45
4	MNSW Life Stage 1 – Egg Stage, complete model.....	51
5	MNSW Life Stage 1 – Egg Stage, omitting links that affect only quailbush ecology. ....	53
6	MNSW Life Stage 2 – Larval Stage, complete model.....	59
7	MNSW Life Stage 2 – Larval Stage, omitting links that affect only quailbush ecology. ....	61
8	MNSW Life Stage 3 – Pupal Stage, complete model.....	65
9	MNSW Life Stage 3 – Pupal Stage, omitting links that affect only quailbush ecology. ....	67
10	Causal relationships affecting nectar source ecology for MNSW Life Stage 4 – Adult Stage.....	71
11	MNSW Life Stage 4 – Adult Stage, complete model.....	79
12	MNSW Life Stage 4 – Adult Stage, omitting links that affect only quailbush or nectar source ecology.....	81

## Attachments

### Attachment

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

# Foreword

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

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

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

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

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

Model building consists of determining system parts, identifying the relationships that link these parts, specifying the mechanisms by which the parts interact, identifying missing information, and exploring the model's behavior (Heemskerk et al. 2003<sup>1</sup>). 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.

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<sup>1</sup> 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](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 things 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 components; no single component 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 MacNeill's sootywing skipper (*Hesperopsis graciellae*) (MNSW) (Lepidoptera:Hesperiidae:Pyrginae), a butterfly. 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 MNSW ecology, the effects of specific stressors, the effects of specific management actions aimed at habitat and species restoration, and the indicators used to measure MNSW habitat and population conditions.

## 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 the characteristics of the resource might change as a result of altering its shaping/controlling factors, including those resulting from management actions.

The CEM applied to MNSW 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 MNSW conceptual ecological model has five core components:

- **Life stages** – These consist of the major growth stages and critical events through which the individuals of a species must pass in order to complete a full reproductive cycle.
- **Life-stage outcomes** – These consist of the biologically crucial outcomes of each life stage, including the number of individuals that survive to enter the next life stage or next age class within a single life stage (recruitment rate), or the number of fertilized eggs produced (fertility rate).

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

- **Critical biological activities and processes** – These consist of activities in which the species engages and 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 of which significantly beneficially or detrimentally affect the rates of the critical 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 properties 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 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 MNSW conceptual ecological model addresses the MNSW population along the flood plain of the lower Colorado River (LCR) within the protected areas along the LCR that currently provide or could provide MNSW habitat under the auspices of the LCR MSCP Habitat Conservation Plan. The purpose of the present effort is not to provide an updated literature review of the ecology of MNSW but to integrate the available information and knowledge into a CEM so it can be used for adaptive management.

No single publication provides a comprehensive review of the literature on MNSW ecology. However, numerous publications by Reclamation biologists, some coauthored with academic scientists, provide a thorough review in aggregate (Wiesenborn 1997, 1999, 2010a, 2010b, 2011, 2012a, 2012b; Nelson and Andersen 1999; Reclamation 2008, 2009, 2013; Wiesenborn and Pratt 2008, 2010; Pratt and Wiesenborn 2009, 2011; Nelson and Wydoski 2013; Nelson et al. 2014, 2015). Except for a single general species account (Reclamation 2008),

**MacNeill’s Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

these publications focus on specific topics related to the LCR MSCP, such as field methods; species abundance, distribution, and behaviors both annually and relative to habitat conditions; preferred host plant characteristics; and preferred nectar sources. NatureServe (2015) provides an additional overview. A separate body of literature addresses the ecology of the MNSW host plant, the quailbush (*Atriplex lentiformis*), summarized by Meyer (2005). The CEM also integrates information from current LCR MSCP research projects and the expert knowledge of LCR MSCP biologists.

The MNSW conceptual ecological model distinguishes and assesses four life stages, most with only a single associated life-stage outcome, as follows (table ES-1):

Table ES-1.—Outcomes of each of the four life stages of MNSW

Life stage	Life-stage outcome
1. Egg (from all broods in a year)	<ul style="list-style-type: none"> <li>• Survivorship</li> </ul>
2. Larval (includes all molts (aka instars) from all broods in a year)	<ul style="list-style-type: none"> <li>• Survivorship</li> </ul>
3. Pupal (from all broods in a year)	<ul style="list-style-type: none"> <li>• Survivorship</li> </ul>
4. Adult (of all broods in a year)	<ul style="list-style-type: none"> <li>• Survivorship to mating</li> <li>• Reproductive output rate</li> <li>• Dispersal rate</li> </ul>

The model distinguishes 7 critical biological activities and processes relevant to 1 or more of these life stages, 15 habitat elements relevant to 1 or more of these critical biological activities and processes for 1 or more life stages, and 6 controlling factors that affect 1 or more of these habitat elements. Because the protected areas managed under the LCR MSCP comprise a highly regulated system, the controlling factors almost exclusively concern human activities.

The seven critical biological activities and processes identified across all life stages are: contamination and infection, feeding/watering, hiding/resting, mating, ovipositing, physiological stress, and predation. The 15 habitat elements identified across all life stages are: chemical contaminants, competitors, fire regime, infectious agents, inundation regime, nectar sources, predators, quailbush litter condition, quailbush patch distribution, quailbush patch size and structure, quailbush shrub condition, scientific study, soil moisture, soil nitrogen, and soil salinity. The six controlling factors identified across all habitat elements

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

are: offsite land management and use, onsite fire management, onsite vegetation management, onsite visitation and study, onsite water management, and reach-scale water management.

## **KEY RESULTS**

The assessment of the causal relationships among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes indicates the following strong (high-magnitude) causal relationships:

- Three controlling factors – offsite land management and use, onsite vegetation management, and onsite water management – have consistently high-magnitude effects on multiple habitat elements across all life stages. Onsite fire management and reach-scale water management have high-magnitude effects on a single habitat element each, the fire regime and the inundation regime, respectively.
- Two habitat elements – quailbush patch size and structure and quailbush shrub condition – have consistently high-magnitude effects on multiple critical biological activities and processes across all life stages. Quailbush litter condition affects two critical biological activities and processes across two life stages. The potential array of predator species present in MNSW habitat sites and their numbers affects one critical biological process – predation – in all four life stages. The types, abundances, and spatial and temporal distributions of nectar sources strongly affect adult feeding/watering success.
- Seven habitat elements have high-magnitude direct effects on other habitat elements and thereby strongly *indirectly* affect one or more critical biological activities and processes across one or more MNSW life stages. Specifically, the fire regime has a high-magnitude effect on nectar sources; quailbush litter condition strongly affects the potential array of predator species present in MNSW habitat sites and their numbers, and it also may strongly affect soil nitrogen; quailbush shrub condition and quailbush patch size and structure strongly affect each other, and both strongly affect the potential array of predator species present in MNSW habitat sites and their numbers; soil moisture strongly affects nectar sources, quailbush patch size and structure, quailbush shrub condition, and soil salinity; soil nitrogen strongly affects nectar source conditions; and soil salinity strongly affects quailbush shrub condition. One might also expect that the fire regime has a high-magnitude effect on quailbush shrub condition and quailbush patch size and structure. However, quailbush is resistant to fire, can regenerate from adventitious buds following fire, and can rapidly recolonize burn sites through onsite and offsite seed

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

production and dispersal. As a result, wildfires have a lower-magnitude impact on quailbush than on the majority of nectar sources, including saltcedar and mesquite.

- Four critical biological activities potentially strongly affect life-stage outcomes in one or more life stages. Predation and physiological stress potentially strongly affect survivorship in all four life stages. Predation also potentially strongly affects reproductive output. Feeding/watering activities and their success are proposed to strongly affect survivorship among both larvae and adults, and ovipositing activities and their success necessarily affect reproductive output.
- Four critical biological activities and processes have high-magnitude direct effects on other critical biological activities and processes and thereby strongly *indirectly* affect one or more life-stage outcomes across the MNSW life cycle. Specifically, feeding/watering activities and their success potentially strongly affect ovipositing and the rates of physiological stress among larvae and adults; hiding/resting activities and their success potentially strongly affect both predation and physiological stress among pupae, larvae, and adults; and both mating activities and their success and rates of physiological stress affect ovipositing among adults.

The assessment of causal relationships also identified those with high magnitude but low understanding. Two controlling factors – offsite land management and use and onsite vegetation management – have high-magnitude but poorly understood impacts on habitat elements with significant cascading impacts on critical biological activities and processes. Eight habitat elements – the fire regime, predators, quailbush litter condition, quailbush patch distribution, quailbush patch size and structure, quailbush shrub condition, soil moisture, and soil nitrogen – have multiple high-magnitude but poorly understood impacts on other habitat elements, on critical biological activities and processes, or, in one case, directly on a life-stage outcome.

MNSW life-stage outcomes, critical biological activities and processes, and habitat elements may also be shaped by other causal relationships, about which there is not sufficient information to assess link magnitude. The CEM proposes the existence of these relationships based on established ecological principles, information on butterflies or skippers in general, suggestions in the literature on MNSW, or suggestions from experts consulted for this CEM. However, too little is known about these relationships to form hypotheses about link magnitude.

The CEM for MNSW thus, in part, highlights aspects of the ecology of the species already well established or subjects of established research programs. These topics include the close relationships of MNSW ecological dynamics to the ecological dynamics of quailbush, and an array of nectar sources, and the possible

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

relationships of these dynamics to soil conditions. Additionally, the CEM highlights numerous aspects of MNSW ecology that are less well studied but that likely also play significant roles in shaping the abundance and distribution of MNSW within individual habitat patches and across the LCR as a whole. Finally, the CEM highlights aspects of MNSW ecology that, while potentially significant, are too poorly studied to allow for any inferences concerning their importance.

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 MNSW. 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 MacNeill’s sootywing skipper (*Hesperopsis graciellae*) (MNSW) (Lepidoptera:Hesperiidae:Pyrginae), a butterfly (MacNeill 1970). Other common names for this species include MacNeill’s saltbush sootywing. It is a member of Hesperiidae, a family of butterflies commonly called “skippers” (NatureServe 2015). This species is the only invertebrate covered under the Bureau of Reclamation (Reclamation), Lower Colorado River Multi-Species Conservation Program (LCR MSCP), Habitat Conservation Plan (HCP).

The purpose of this model is to help LCR MSCP personnel identify areas of scientific uncertainty concerning MNSW ecology, the effects of specific stressors, the effects of specific management actions aimed at habitat and species restoration, and the indicators used to measure MNSW 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 described below and in attachment 1. (Note: Attachment 1 provides an introduction to the CEM process. We recommend that those unfamiliar with this process read attachment 1 before continuing with this document.)

The CEM addresses the MNSW population along the flood plain of the lower Colorado River (LCR). Specifically, the model addresses MNSW within the conservation areas along the LCR that currently provide or could provide MNSW habitat under the HCP.

MNSW historically occurred along the valleys of the LCR and its tributaries in southeastern California, western Arizona, southern Nevada, and southern Utah (Reclamation 2008). Its range also extended into northwestern Mexico, including the eastern Baja California peninsula (Brown 2004; NatureServe 2015). It presently occurs in scattered locations throughout its historic range, except possibly no longer in Utah (Reclamation 2008; Pratt and Wiesenborn 2011; NatureServe 2015).

No single publication provides a comprehensive review of the literature on MNSW ecology. However, numerous publications by Reclamation biologists, some coauthored with academic scientists, provide a thorough review in aggregate (Wiesenborn 1997, 1999, 2010a, 2010b, 2011, 2012a, 2012b; Nelson and Andersen 1999; Reclamation 2008, 2009, 2013; Wiesenborn and Pratt 2008, 2010; Pratt and Wiesenborn 2009, 2011; Nelson and Wydoski 2013; Nelson et al. 2014, 2015). Except for a single general species account (Reclamation 2008), these publications focus on specific topics related to the LCR MSCP, such as field methods; species abundance, distribution, and behaviors both annually and relative to habitat conditions; preferred host plant characteristics; and preferred

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

nectar sources. NatureServe (2015) provides an additional overview. The CEM also integrates information from current LCR MSCP research projects and the expert knowledge of present and former LCR MSCP biologists.

A separate body of literature addresses the ecology of the sole host plant of the species, the quailbush (*Atriplex lentiformis*), Chenopodiaceae, summarized by Meyer (2005). MNSW depend on this species for egg laying, larval feeding and sheltering, pupal maturation, and adult sheltering and mating. However, adult MNSW mostly obtain their food nectar from other species and have been observed only rarely feeding on quailbush nectar (Nelson et al. 2015). As summarized by Wiesenborn and Pratt (2008) and Meyer (2005), quailbush is a large blue- or grey-green, dome-shaped shrub that can reach heights approaching 3 meters (m). It is most likely wind pollinated, generally dioecious, adapted to hot, arid environments, and grows best in saline flood plain soils with high groundwater tables. It fixes nitrogen through the actions of root-symbiotic bacteria and produces numerous thick leaves, 1–5 centimeters long and 0.6–3.8 centimeters wide, covered in fine scales on numerous slender branches.

Readers are referred to the background literature for information on MNSW taxonomy and identifying characteristics. The purpose of the present effort 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 introduces the underlying concepts and structure of the CEM. Chapter 2 presents a life-stage model for MNSW that provides the framework for the CEM. Succeeding chapters present and explain the CEM for MNSW along the LCR and identify potentially important causal relationships for management, monitoring, and research consideration.

## **CONCEPTUAL ECOLOGICAL MODEL PURPOSES**

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

CEMs explicitly identify: (1) the variables or attributes that best characterize resource conditions, (2) the factors that most strongly shape or control these variables under both natural and altered (including managed) conditions, (3) the

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

character, strength, and predictability of the ways in which these factors do this shaping/controlling, and (4) how the characteristics of the resources vary as a result of the interplay of its shaping/controlling factors.

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

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

## **CONCEPTUAL ECOLOGICAL MODEL STRUCTURE**

The CEM methodology used here expands on that developed for the Sacramento-San Joaquin River Delta Regional Ecosystem Restoration Implementation Plan (DiGennaro et al. 2012). The expansion incorporates recommendations of Wildhaber et al. (2007, 2011), Kondolf et al. (2008), and Burke et al. (2009) to provide greater detail on causal linkages and outcomes and explicit demographic notation in the characterization of life-stage outcomes (McDonald and Caswell 1993). Attachment 1 provides a detailed description of the methodology.

The CEM methodology applied here produces a “life history” model, as is common for CEMs focused on an individual species (Wildhaber et al. 2007, 2011). That is, the methodology distinguishes the major life stages or events

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

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., egg to larval) or 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 MNSW 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 that survive to enter or “transition to” the next life stage (e.g., transition from pupal to adult) or the next age class within a single life stage (recruitment rate), 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 butterfly species in one or more life stages may include feeding, mating, ovipositing, and avoiding predators. Critical biological activities and processes typically are “rate” variables.
- **Habitat elements** – These consist of the specific habitat conditions, the quality, abundance, and spatial and temporal distributions of which significantly affect the rates of the critical activities and processes for each life stage. Taken together, the suite of natural habitat elements for a life stage is called the “habitat template” for that life stage. Defining the natural habitat template may involve estimating specific thresholds or ranges of suitable values for particular habitat elements outside of which one or more critical life activities or processes no longer fully support desired life-stage outcome rates – if the state of the science supports such estimates.

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

- **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.” A hierarchy of such factors may affect the system at different scales of time and space (Burke et al. 2009). For example, MNSW require quailbush to complete their life cycle. Quailbush require soils with a particular range of texture, moisture, and salinity. The distributions of such soils depends on factors such soil histories, groundwater elevations, precipitation, and inundation, which in turn may depend on factors such as past flood plain geomorphic dynamics and recent operations of water management systems, which in turn depend on watershed and valley geology, flood plain vegetation overall, and climate.

The CEM identifies these five types of core components and the causal relationships among them that affect life-stage outcome rates. Further, the CEM assesses each causal linkage based on four properties 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 and 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 and processes). In addition, the CEM for each life stage highlights areas of scientific uncertainty concerning these causal relationships and the effects of specific management actions aimed at these relationships. 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 – MNSW 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 MNSW in the LCR on which to build the CEM. The MNSW life cycle resembles that of all butterflies, with distinct egg, larval, pupal, and adult stages. The details of each of these four life stages differ between MNSW and other butterflies but are similar between MNSW and other skippers (Family:Hesperiidae).

### PROPOSED LIFE STAGES FOR MACNEILL’S SOOTYWING SKIPPER

The literature identifies four MNSW life stages, most with only a single life-stage outcome, as follows and summarized in table 1 (also see figure 1). The life stages are numbered sequentially beginning with the egg stage:

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

Life stage	Life-stage outcome
1. Egg	<ul style="list-style-type: none"><li>• Survivorship</li></ul>
2. Larval	<ul style="list-style-type: none"><li>• Survivorship</li></ul>
3. Pupal	<ul style="list-style-type: none"><li>• Survivorship</li></ul>
4. Adult	<ul style="list-style-type: none"><li>• Survivorship to mating</li><li>• Reproductive output rate</li><li>• Dispersal rate</li></ul>

#### Egg Stage

This life stage includes the eggs from all broods in a year (see discussion of broods under “Adult Stage,” below). Multiple eggs may occur on a single quailbush plant (Wiesenborn and Pratt 2008). However, the studies reviewed for this CEM do not indicate how many females may contribute to such multiple occurrences. Wiesenborn and Pratt (2008) found that plants with at least one MNSW egg present had an average of 3.3 eggs per plant, range 1–8, although only 1 or 2 eggs were observed on any single leaf (Wiesenborn 2012a). MNSW eggs thus experience threats to their survival (e.g., predation) largely individually,

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

one egg at a time, rather than collectively as egg batches. No studies reviewed for this CEM discuss time to hatching or rates of hatching success or discuss factors that may affect these variables. Wiesenborn (2012a) reports that, of 15 eggs tracked in a controlled study of MNSW eggs on quailbush, 4 (27 percent) survived to adulthood. However, the report does not provide data separately on egg, larval, and pupal survivorship or on causes of mortality. The egg life stage has a single life-stage outcome, designated  $S_E$  on figure 1, survivorship over the course of the life stage.

## **Larval Stage**

This life stage includes all instars for all larvae (caterpillars) produced by all broods in a year (see discussion of broods under “Adult Stage,” below). MNSW larvae may be active (e.g., feeding) between April 1 and November 30 (Reclamation 2009). They live exclusively on quailbush, on the leaves of which they exclusively feed and with which they build shelters (Greeney and Jones 2003; Reclamation 2009, 2013; Pratt and Wiesenborn 2011; Greeney et al. 2012; Wiesenborn 2012a). The shelters consist of cut leaf sections for smaller larvae, or one or more entire folded leaves for larger, older larvae, held together with silk threads (Pratt and Wiesenborn 2011; Nelson et al. 2015). The larvae remain in their shelters when not feeding, which may be most of the day (Pratt and Wiesenborn 2011; Nelson et al. 2015). The literature reviewed for this CEM does not report on whether larval activity varies with time of day.

Larval survival depends in part on the quality of the leaves on which they feed. For example, host plants with a leaf-water content < 64 percent and a leaf-nitrogen content < 3.2 percent do not fully support larval survival or development (Reclamation 2013). Conversely, Nelson et al. (2015) note and cite studies that “[n]itrogen content of leaf matter is correlated with increased lepidopteran caterpillar growth rates” in general and that “[h]igher leaf-water content is also associated with increased rates of insect larval development.”

The literature reviewed for this CEM does not characterize MNSW larvae as highly mobile, implicitly suggesting that individual larvae remain on their natal plant through all instars. MNSW probably overwinter as larvae from the last brood of the year (Wiesenborn 2010a), but the subject does not appear to have been formally assessed. NatureServe (2015) states that the species overwinters “...probably as fully fed larvae as in related genera like *Staphylus* and *Pholisora*.” Wiesenborn (2010a) states that MNSW larvae overwinter in plants. Overwintering presumably takes place within a folded leaf structure, since MNSW larvae spend most of their time in such leaf shelters. The literature reviewed for this CEM does not report on the environmental factors, such as air temperature or photoperiod, which may trigger the initiation or termination of winter dormancy (diapause). Richard Wydoski, a Reclamation biologist (2015,

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

personal communication), notes that MNSW sites are not monitored through November. Consequently, the observational record does not indicate how late in the season MNSW larvae remain active. The literature reviewed for this CEM also does not report on the duration of the larval stage let alone the duration of individual instars. The life stage has a single life-stage outcome, designated  $S_L$  on figure 1, survivorship over the course of the life stage.

## **Pupal Stage**

This life stage includes all pupae from all broods in a year (see discussion of broods under “Adult Stage,” below). The literature reviewed for this CEM does not definitively indicate where MNSW pupation takes place. Pratt and Wiesenborn (2011) state that pupation takes place in a leaf shelter (see “Larval Stage,” above). However, it is not clear whether this leaf structure lies within the quailbush or beneath: Pratt and Wiesenborn (2009) state that larvae “... likely crawl down to the base of the plant to pupate in leaf litter,” but base this suggestion only on observations of MNSW reared by the senior author in laboratory cages. However, quailbush shrubs are generally evergreen except during severe drought (Meyer 2005). Consequently, they could provide suitable sites for pupation within the canopy as well. The literature reviewed for this CEM does not discuss whether overwintering larvae pupate in a different setting than do the larvae from the subsequent broods in a year. The literature also does not report on the duration of pupation or factors that may affect pupal survivorship or the duration of pupation. The life stage has a single life-stage outcome, designated  $S_P$  on figure 1, survivorship over the course of the life stage.

## **Adult Stage**

This life stage includes all individuals that emerge as adults in a year, beginning with those that emerge from the pupae from the last brood of the previous year. MNSW are typically at least bivoltine: Two flights typically occur in a single year, the first between April and May, and the second between July and October (NatureServe 2015), with flying adults sometimes observed in March and June as well (Nelson and Andersen 1999). Behaviors within patches of quailbush include flying within and between individual quailbush shrubs, chasing or being chased by other sootywings, basking (stationary with wings open), perching (stationary with wings closed), landing on and probing potential nectar sources with proboscis, mating, and ovipositing (Pratt and Wiesenborn 2009; Nelson et al. 2015). Flying movement among MNSW adults, as among all skippers, is typically described as fluttering and skipping.

MNSW adults spend most of their time within the shaded domes of quailbush shrubs, particularly during the hottest hours of the day (Wiesenborn 1999; Pratt

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

and Wiesenborn 2009; Nelson et al. 2014, 2015). They feed on the floral nectar of nearby saltcedar (*Tamarix ramosissima*) (non-native), salt heliotrope (*Heliotropium curassavicum*) (native), arrowweed (*Pluchea sericea*) (native), western (or sea) purslane (*Sesuvium verrucosum*) (native), alkali mallow (*Malvella leprosa*) (native), honey mesquite (*Prosopis glandulosa*) (native), screwbean mesquite (*Prosopis pubescens*) (native), common purslane (*Portulaca oleacea*) (non-native), and alfalfa (*Medicago sativa*) (non-native) (Wiesenborn 1997; Pratt and Wiesenborn 2009, 2011; Reclamation 2013; Nelson et al. 2014, 2015). Additionally, MNSW adults probably feed on honey mesquite extrafloral nectar (Wiesenborn 1997; Nelson et al. 2014, 2015) and may feed on quailbush nectar as well (Nelson et al. 2015).

Fecundity may vary with the nutritional quality (density) of the nectar (Nelson and Andersen 1999; Wiesenborn and Pratt 2010; Pratt and Wiesenborn 2011). MNSW oviposit on both the upper- and undersides of leaves and apparently select leaves for their moisture content, which correlates strongly with leaf nutritional value (Wiesenborn and Pratt 2008; Reclamation 2009, 2013; Pratt and Wiesenborn 2011; Wiesenborn 2012a, 2012b; Nelson et al. 2015). Ovipositing usually occurs close to the mid-vein of the leaf (Nelson et al. 2015).

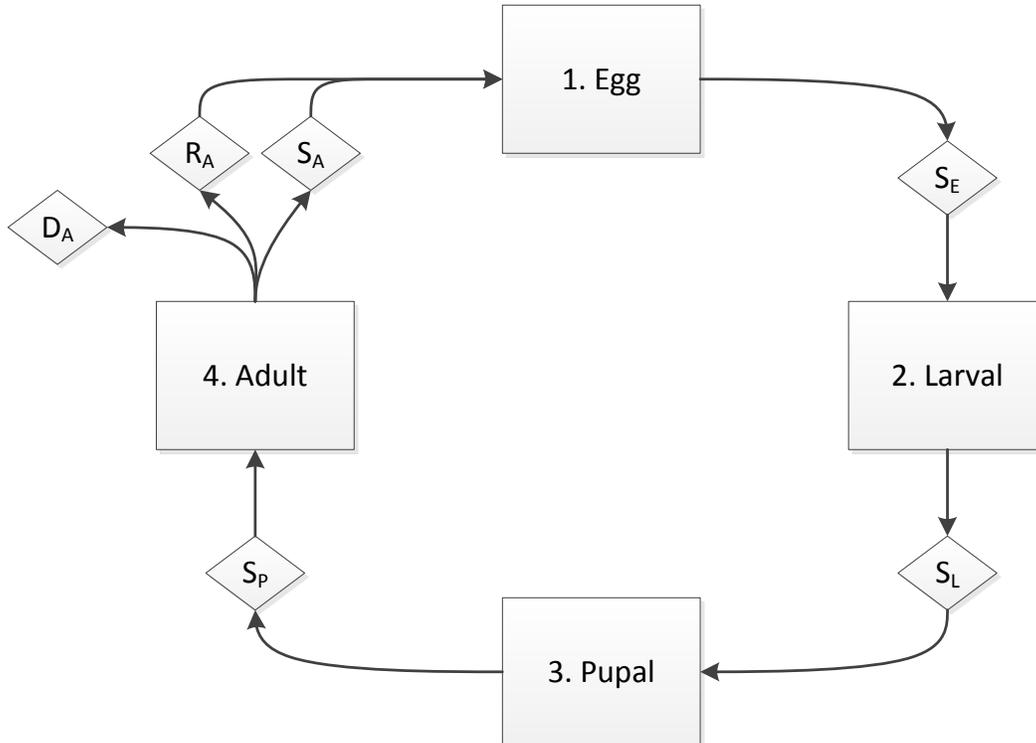
The literature reviewed for this CEM does not discuss adult lifespan other than to note (Nelson et al. 2014) that adult life expectancy is unknown. Richard Wydoski, a Reclamation biologist (2015, personal communication), suggests it could be roughly only 2 weeks.

MNSW adults also episodically colonize unoccupied habitat patches and genetically mix across the landscape by dispersing from occupied habitat. Under natural conditions, the distribution, composition, and quality of habitat patches (see chapters 3 and 4) would have shifted across the LCR landscape as a result of creative and destructive natural disturbances such as wildfire, flooding, changing water table elevations, and vegetative succession (Nelson and Andersen 1999; Elmore et al. 2003; MacNally et al. 2004; Meyer 2005; Stromberg et al. 2007; Calvert 2008; Conway et al. 2010; Pratt and Wiesenborn 2011; Wiesenborn 2012b; NatureServe 2015). MNSW therefore are adapted to dispersing to colonize or recolonize patches following disturbances. However, today's highly altered landscape poses significant challenges to the ability of MNSW to disperse among occupied and/or unoccupied habitat patches (Nelson and Andersen 1999; Reclamation 2009; Wiesenborn 2010a, 2012b; Pratt and Wiesenborn 2011; Nelson et al. 2014, 2015). The literature reviewed for this CEM does not contain any data on MNSW dispersal distances (Nelson et al. 2014), and no studies have yet been conducted to examine possibilities for manually assisting dispersal and colonization.

The MNSW adult life stage has three life-stage outcomes: (1) the rate of survivorship of adults long enough following emergence to mate, designated  $S_A$  on figure 1; (2) the rate of production of viable eggs per surviving adult in a year,

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

designated  $R_A$  on figure 1; and (3) the rate of successful dispersal of adults to other habitat patches, designated  $D_A$  on figure 1. (Theoretically, the CEM could combine the first two outcomes into a single outcome, the rate of production of viable eggs among all adults in a year. However, field studies of MNSW routinely assess adult abundance but not ovipositing output per individual female. The CEM therefore distinguishes the two components of overall reproductive output so that it can represent the conditions that affect adult abundance separately from the conditions that affect reproductive output per adult.)



**Figure 1.—Proposed MNSW life history model.**

Squares indicate the life stage, and diamonds indicate life-stage outcomes.  $S_E$  = egg stage, life-stage outcome;  $S_L$  = larval stage, life-stage outcome;  $S_P$  = pupal stage life-stage outcome;  $S_A$  = the rate of survivorship of adults long enough following emergence to mate;  $R_A$  = the rate of production of viable eggs per surviving adult in a year; and  $D_A$  = the rate of successful dispersal of adults to other habitat patches.

# 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 activities and processes are “rate” variables.

The model identifies seven critical activities and processes that may either directly or indirectly affect one or more MNSW life stages. Some of these activities or processes differ in their details among life stages. For example, MNSW of different life stages differ in their hiding and resting behaviors and in their exposures to different potential sources of physiological stress. However, grouping activities or processes into broad types across all life stages makes it easier to compare the individual life stages to each other across the entire life cycle. Table 2 lists the seven critical activities and processes and their distributions across the four MNSW life stages. Each critical biological activity and process listed in table 2 directly or indirectly affects one or more outcomes for each indicated life stage.

Table 2.—MNSW critical biological activities and processes by life stage

Life stage →	Egg	Larval	Pupal	Adult
↓ Critical biological activity and process				
Contamination and infection	X	X	X	X
Feeding/watering		X		X
Hiding/resting		X	X	X
Mating				X
Ovipositing				X
Physiological stress	X	X	X	X
Predation	X	X	X	X

The following paragraphs discuss the seven critical activities and processes in alphabetical order.

## CONTAMINATION AND INFECTION

Theoretically, MNSW are vulnerable to contamination by anthropogenic chemicals and to infection by agents such as bacteria, fungi, and parasites, as

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

are all insects. Anthropogenic chemicals may disrupt insect health and/or impair growth, development, or reproduction. Similarly, infections may kill or weaken individual insects or disrupt growth, development, or reproduction.

It is recognized in the LCR MSCP Habitat Conservation Plan (Reclamation 2004) that anthropogenic chemicals may be applied in its conservation areas to help establish or maintain desired vegetation for covered bird species. However, the HCP states that LCR MSCP efforts will include "...methods that minimize the need for application of herbicides, pesticides, and fertilizers.... Use of pesticides is not a covered activity. Pesticides used to establish and maintain LCR MSCP habitats...will be applied in accordance with EPA restrictions." The LCR MSCP Habitat Conservation Plan allows for the use of pesticides to control unwanted ant species in conservation areas and the use of herbicides to control non-native plants (Reclamation 2014). However, the literature reviewed for this CEM does not record any instances in which LCR MSCP use of herbicides, pesticides, or fertilizers has affected any MNSW habitat sites.

Locations with or potentially suitable for MNSW habitat also occur in former agricultural areas or adjacent to presently actively farmed lands. For example, both the Palo Verde Ecological Reserve and Cibola Valley Conservation Area (CVCA) contain occupied and potential additional MNSW habitat (Nelson et al. 2014). Both conservation areas incorporate former agricultural fields and lie immediately adjacent to farmlands actively in use, for example, to produce alfalfa and cotton. Chemical use on the adjacent fields potentially could result in contamination of MNSW habitat either through wind transport of sprayed chemicals or through chemicals leaching into shallow groundwater. Reclamation biologists (R. Wydoski 2015 and S.M. Nelson 2015, personal communications) anecdotally reported one instance in which cottonwoods exhibited damage consistent with herbicide exposure in a LCR MSCP conservation area, although not specifically in MNSW habitat. James Knowles (2015, personal communication) reports that farmers along the LCR may apply some pesticides (insecticides, fungicides, and bactericides) by aerial spraying, and drift from aerially sprayed pesticides potentially could reach MNSW habitat sites. Cotton farmers may also aerially apply some herbicides, for example, to promote faster leaf drop prior to harvesting. Neonicotinoid pesticides, widely used on alfalfa and cotton, are known to harm insects feeding on floral nectar in fields to which these pesticides have been applied and can contaminate groundwater as well (Goulson 2013; Cutler et al. 2014; Pecenka and Lundgren 2015).

The literature records no instances in which contaminants from adjacent farmlands are known or suspected to have affected any MNSW habitat sites. On the other hand, MNSW adults travel outside their natal quailbush habitat sites to feed, including in nearby alfalfa fields (see chapter 3, "Feeding/Watering) where they could be exposed to these contaminants. At a larger spatial scale, pesticide-treated fields theoretically could present obstacles to MNSW adult dispersal. The CEM therefore must at least recognize the possibility of interactions between

**MacNeill’s Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

MNSW and agricultural chemicals as a result of exposure both within agricultural fields and within MNSW habitat sites into which agricultural chemicals have dispersed. Chapter 4 also discusses the types of chemical contaminants to which MNSW might be exposed along the LCR valley and the potential consequences of chemical contamination for quailbush shrub condition.

Parasitic infections are a common challenge for butterflies in general, to which all species have evolved arrays of defenses (Gross 1993; Greeney and Jones 2003; Altizer and de Roode 2010; Greeney et al. 2012). MNSW larval defenses, for example, include the use of leaf shelters. In turn, would-be attackers, such as different species of parasitoid flies and wasps, have evolved adaptations to attacking particular host butterfly species. However, the literature reviewed for this CEM does not identify any particular parasitoid species that use MNSW as their host. The literature reviewed also does not provide information on types or frequencies of evidence for parasitism among MNSW of any life stage. Wiesenborn (2010a) specifically noted a need for studies of parasitism and predation on MNSW to support habitat conservation.

## FEEDING/WATERING

MNSW larvae feed exclusively on quailbush leaves, while MNSW adults feed on floral or extrafloral nectar from a variety of plant species (table 3). MNSW larvae and adults have distinct repertoires of feeding behaviors. Feeding success in both life stages depends on food resource quality and availability. MNSW larvae and adults obtain all or most of their water from their foods alone.

Table 3.—MNSW nectar sources

Species	Origin <sup>1</sup>	Floral	Extra-floral
<i>Tamarix ramosissima</i> , saltcedar	O	X	
<i>Heliotropium curassavicum</i> , salt heliotrope	N	X	
<i>Pluchea sericea</i> , arrowweed	N	X	
<i>Sesuvium verrucosum</i> , western purslane	N	X	
<i>Malvella leprosa</i> , alkali mallow	N	X	
<i>Prosopis glandulosa</i> , honey mesquite	N	X	X
<i>Prosopis pubescens</i> , screwbean mesquite	N	X	X
<i>Portulaca oleacea</i> , common purslane	O	X	
<i>Medicago sativa</i> , alfalfa	O	X	
<i>Bebbia juncea</i> , sweetbush	N	X	
<i>Coriandrum sativum</i> , Chinese parsley	O	X	
<i>Atriplex lentiformis</i> , quailbush	N	X	

<sup>1</sup> “N” = native, and “O” = non-native.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

MNSW larvae feed only outside their leaf shelters. Their feeding can cause extensive damage to individual leaves, which enhances field detection (Pratt and Wiesenborn 2011; Wiesenborn 2012a; Nelson et al. 2014). They survive and develop best on leaves with a leaf-water content > 64 percent and a leaf-nitrogen content > 3.2 percent, the latter measured as the dry weight of total Kjeldahl nitrogen relative to leaf dry weight (Wiesenborn and Pratt 2008; Reclamation 2009, 2013; Nelson et al. 2015).

MNSW adults leave the cover of quailbush vegetation to find and feed on nectar sources (Wiesenborn and Pratt 2008; Pratt and Wiesenborn 2011). The list of MNSW adult nectar sources in table 3 follows Wiesenborn (1997, 2010a, 2010b, 2011), Pratt and Wiesenborn (2009, 2011), Reclamation (2013), and Nelson et al. (2014, 2015). Wiesenborn (1997) proposed that adult MNSW do not feed on quailbush flowers simply because they are wind pollinated and therefore do not produce nectar. However, Meyer (2005) notes that, while members of the genus *Atriplex* generally are wind pollinated, there is no specific evidence of this for quailbush (*Atriplex lentiformis*) and Nelson et al. (2015) subsequently in fact observed MNSW feeding on quailbush floral nectar. Table 3 lists floral feeding on Chinese parsley (*Coriandrum sativum*) based on Arizona Game and Fish Department (2003) and on sweetbush (*Bebbia juncea*) based on Wiesenborn (1997), and it lists extrafloral feeding on mesquite based on Wiesenborn (1997). Pratt and Wiesenborn (2009) also suggested that MNSW adults may feed on insect secretions known as “honeydew,” based on observations of MNSW flying in non-blooming *Baccharis* spp. bushes where “... many wasps and other insects were observed feeding upon this insect secretion.”

The first six species listed in table 3 appear in decreasing order of the frequency of MNSW landings on their flowers reported in a study by Pratt and Wiesenborn (2009). However, this ordering simplifies a complex set of relationships, as MNSW adult selection of nectar sources for feeding varies over the annual cycle. They feed on salt heliotrope dominantly beginning in April, but ending late in June, on arrowweed, peaking late June-early July, and on saltcedar, peaking late August (Pratt and Wiesenborn 2009).

MNSW adults feed more often later in the day (Pratt and Wiesenborn 2009), at which time they leave the cover of quailbush vegetation to find and feed on “nearby” nectar sources (Wiesenborn and Pratt 2008; Pratt and Wiesenborn 2011). However, the literature reviewed for this CEM provides little data on foraging distances. Wiesenborn (1997) frequently observed individuals flying across distances of approximately 4 m between quailbush shrubs and mesquite (potentially to feed on extrafloral nectar), which may indicate a common foraging distance. In contrast, the same study also reported MNSW “...feeding at flowers of *Bebbia juncea* (Benth.) (Asteraceae) ~ 0.25 km from the study site and the only insect-pollinated plants in flower in the vicinity.”

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Studies of MNSW feeding on salt heliotrope indicate that they select flowers based on the appearance of the flower petals in visible and ultraviolet light (Wiesenborn 2010b, 2011). Feeding duration varies from < 10 seconds to > 60 seconds (Wiesenborn and Pratt 2010), although Nelson et al. (2015) observed a female feeding for 11 minutes on a single alfalfa plant. Females spend more time feeding than do males, at least on the heavily studied salt heliotrope (Wiesenborn and Pratt 2010). Unlike the males, females ingest significant quantities of nectar, preferentially select flowers with higher nectar sugar content, and spend more time feeding when flowers have lower sugar content – all indications that female, but not male, feeding is strongly guided by a quest for nutrition (Wiesenborn 2010a, 2011; Wiesenborn and Pratt 2010). Nelson et al. (2015) also suggest that adult females may feed more often, and seek out higher-quality nectar, if their natal quailbush provided them (as larvae) with leaves of lower nutritional quality.

MNSW adults appear to obtain most or all of their water from nectar. Puddling (drinking from moist soil and the edges of open water) is a common butterfly behavior. However, none of the field studies reviewed for this CEM report puddling by MNSW adults along the LCR despite the presence of opportunities for such behavior (Pratt and Wiesenborn 2009; Nelson et al. 2015). For example, Pratt and Wiesenborn (2009) noted that, "... [d]espite the presence of mud at several locations where sootywings were common, mud puddling was not observed. This mud could have been a good source of moisture for these sootywings, but perhaps it was too alkaline."

## **HIDING/RESTING**

MNSW larvae and adults have distinct repertoires of behaviors for resting and for shielding themselves from visibility and exposure to potentially threatening environmental conditions. As summarized in chapter 2, MNSW larvae hide and rest in their shelters of folded leaf sections or folded leaves, and adults spend most of their time within the canopy of individual quailbush shrubs and shrub thickets.

MNSW larval shelters consist of cut leaf sections for smaller larvae, or one or more entire folded leaves for larger (older) larvae, held together with silk threads (Pratt and Wiesenborn 2011; Nelson et al. 2015). This is a common shelter type among HesperIIDae, the family of MNSW (Greeney and Jones 2003). The larvae remain in their shelter when not feeding, which may be most of the day (Pratt and Wiesenborn 2011; Nelson et al. 2015). The literature reviewed for this CEM does not report on whether larval activity varies with time of day.

HesperIIDae larval leaf shelters in general, and MNSW larval leaf shelters in particular, are thought to serve several functions, including reducing parasitism and predation, and providing shade, humidity, or protection from desiccation

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

(Greeney and Jones 2003; Pratt and Wiesenborn 2011; Greeney et al. 2012; Nelson et al. 2015). Different species form their shelters in different ways to achieve additional functions such as entry and exit, water drainage, air circulation, and waste disposal (Greeney and Jones 2003).

MNSW adults spend most of their time within the quailbush canopy, particularly during the hottest hours of the day, and their frequency of movement – both within and outside the canopy – varies with air temperature (less movement at both high and low temperatures) (Wiesenborn 1999; Pratt and Wiesenborn 2009; Nelson et al. 2014, 2015). The shade of the canopy appears to help MNSW tolerate high air temperatures (Wiesenborn 1999, 2010a) to which they may be less physiologically adapted than some other butterfly species (Wiesenborn 1999). MNSW may also prefer quailbush located near trees, the shade of which may provide some additional protection against the heat (Wiesenborn 1997; Pratt and Wiesenborn 2011; Nelson et al. 2014). Theoretically, adult MNSW within quailbush canopy also would be less visible to predators such as insectivorous birds and flying insects overhead. However, the literature reviewed for this CEM provides no information on potential predators on MNSW of any life stage (see “Predation,” below). Wiesenborn (2010a) notes this lack of information on predation (and parasitism) as a significant gap in knowledge of the species.

MNSW adults do sometimes rest above the quailbush canopy, specifically when basking. MNSW bask – rest with wings open – in the open, in sunlight, presumably to raise their body temperature when the air is cool, and this behavior decreases as daytime temperatures increase over the course of each day and over the course of each season (Pratt and Wiesenborn 2009). In contrast, MNSW perch – rest with wings closed – in the shade of the quailbush canopy, and this behavior becomes more frequent as the daytime temperature increases up to some threshold, above which perching behavior becomes less frequent (Pratt and Wiesenborn 2009).

## **MATING**

The literature reviewed for this CEM provides no descriptions of MNSW mating behavior. Pratt and Wiesenborn (2009) and Nelson et al. (2015) included mating among the behaviors they attempted to record in their field studies but do not report on the results. Pratt and Wiesenborn (2009) more generally note that MNSW males actively patrol for females and do so most intensively close to the ground above the leaf litter beneath quailbush shrubs. The authors suggest that this pattern of patrolling would increase male chances of encountering females as the latter emerge from their pupae if they are in the litter (see chapter 2, “Pupal Stage”), all under the protective shade of the shrubs. As noted earlier, however (see chapter 2, “Pupal Stage”), the evidence is weak for where MNSW pupate. Pratt and Wiesenborn (2009) also recorded MNSW adults chasing each other as

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

the third most common activity among adults. They do not distinguish circumstances that might indicate different reasons for the chasing, such as males chasing males in competition for a female. However, their description of male patrolling suggests that the chasing behavior is territorial among males in search of mates.

## **OVIPOSITING**

MNSW females oviposit only on quailbush; eggs and larvae artificially placed on other related species of *Atriplex* fail (Pratt and Wiesenborn 2009; Wiesenborn 2012a). Investigations strongly suggest that, among quailbush shrubs in a patch, MNSW females select plants for ovipositing based on the size and condition of the plant, select leaves for ovipositing based on leaf condition and position within the plant, and select only a limited range of locations on an individual leaf for ovipositing. Specifically:

- Wiesenborn and Pratt (2008) (see also Reclamation 2009) found eggs consistently only on plants that met three criteria: canopy diameter > 1.6 m, leaf-water content > 64 percent, and leaf-nitrogen content (dry weight of total Kjeldahl nitrogen as percent of dry leaf weight) > 3.2 percent. They also found that the minimum number of eggs deposited on a plant increased with increasing canopy diameter, leaf moisture, and/or leaf nitrogen above these threshold values, but the maximum number of eggs did not. The study detected eggs on plants that did not meet all three criteria but with decreasing probability among plants with smaller canopies, lower leaf-water content, and/or lower leaf-nitrogen content. The minimum criteria for plant selection appeared to be canopy diameter > 1.0 m and leaf-nitrogen content > 2 percent (Wiesenborn and Pratt 2008). Nelson et al. (2014) in turn found that females will use smaller shrubs (“seedlings”) when larger plants are not available so long as the shrubs exhibit suitable leaf conditions. Wiesenborn and Pratt (2008) suggest that the females identify plants suitable for ovipositing based on visual cues such as the greenness of a plant, an indicator of leaf-nitrogen content (see also Nelson et al. 2015). Ongoing LCR MSCP studies are being conducted to test the feasibility of measuring leaf greenness as a way to quantify this indicator (S.M. Nelson 2015, personal communications). Nelson et al. (2015) also found that, with a very high statistical significance, females simply do not lay eggs on plants with more than a small percentage of dry leaves present, another indication of plant lushness. Wiesenborn and Pratt (2008) suggest that female selection of plants for ovipositing based on canopy diameter is a consequence of selection for plants with ample shade, which helps the skippers control their body temperature (Wiesenborn 1999). Pratt and Wiesenborn (2011) further note that MNSW females appear to prefer to

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

lay their eggs on quailbush growing in the shade of trees, another possible indication that shading matters in plant selection for ovipositing. Limited data also suggest that MNSW females oviposit more frequently during the morning and early afternoon (Pratt and Wiesenborn 2009), a window of time that avoids the highest air temperatures of the day while still making it possible to use visual cues for plant selection.

- Wiesenborn and Pratt (2008) suggest that MNSW females use chemosensors in their feet to test individual leaves for moisture and/or volatile compounds indicative of leaf health. Further, Nelson et al. (2015) found eggs distributed only between 0.5 and 2.1 m high within quailbush shrubs, with a mean height of 1.1 m. However, it is not possible to determine from these data whether the pattern of variation in egg presence with height is merely a function of where leaves were available, a consequence of predator removal of eggs from higher and lower branches, and/or evidence of actual height preferences.
- MNSW females oviposit on the upper and undersides of leaves, usually close to the mid-vein near the center of the leaf (Pratt and Wiesenborn 2011; Nelson et al. 2015).

## **PHYSIOLOGICAL STRESS**

MNSW in every life stage are vulnerable to physiological stress resulting from disease, inundation, wildfire, and exposure to harmful temperature extremes, chemicals, and winds. As noted earlier in this chapter, MNSW larvae and adults display a range of behaviors for avoiding or escaping potentially stressful conditions (see “Feeding/Watering,” “Hiding/Resting,” and “Ovipositing,” above). Additionally, as also discussed (see “Ovipositing,” above), adult females seeking sites for ovipositing appear to select locations within quailbush shrubs and select shrubs within vegetation patches that provide shelter from a range of potentially stressful conditions. MNSW appear to be particularly sensitive to high elevated temperatures (Wiesenborn 1999) and display a range of behaviors that reduce their exposure – or the exposure of their eggs, pupae, and larvae – to the hottest temperatures of the day and season (see “Feeding/ Watering,” “Hiding/Resting,” and “Ovipositing,” above).

MNSW also hide within quailbush canopies when wind speeds rise: Pratt and Wiesenborn (2011) note that large quailbush shrubs protect MNSW adults from wind. Nelson et al. (2014) cite studies suggesting that butterflies will remain out in the open without seeking shelter (and therefore remain detectable) in winds speeds “...up to five (18–24 miles/hr, 29–38 km/hr) on the Beaufort scale.” However, the surveys of MNSW habitat reported by Nelson et al. (2014, 2015) only “...occurred at wind speeds that were less than or equal to a light breeze

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

(< 7mph (11.3 km/hr), a 2 on the Beaufort wind force scale.” The available data thus do not indicate the magnitudes of winds that might cause MNSW to seek shelter from the wind.

However, MNSW larvae or adults may be unable to avoid or escape some physiologically stressful conditions or, in the case of ovipositing females, anticipate the occurrence of such conditions. Unavoidable or inescapable physiological stresses can result in bodily damage or death. Examples of potential conditions that could result in unavoidable or inescapable physiological stress include patch-scale and larger-scale disturbances such as wildfire; flooding, which can drown pupae in the leaf litter below shrubs and also eggs and larvae on lower branches, depending on flood depth; and extreme winds (Nelson and Andersen 1999; Elmore et al. 2003; MacNally et al. 2004; Meyer 2005; Stromberg et al. 2007; Calvert 2008; Conway et al. 2010; Pratt and Wiesenborn 2011; Wiesenborn 2012b; Nelson et al. 2014; NatureServe 2015) as discussed in chapter 4.

## **PREDATION**

MNSW in every life stage presumably are vulnerable to predation by both invertebrates and vertebrates, as are all butterflies (Greeney et al. 2012). As noted earlier, MNSW behaviors such as larval use of leaf shelters likely indicate adaptations to both predation and parasitism (Greeney and Jones 2012). Wiesenborn and Pratt (2008) also suggest that “... [m]ore rapid development increases larval survival by reducing exposure to predators and parasites.” However, the literature reviewed for this CEM provides no evidence or even suggestions concerning which species may prey on MNSW in any life stage. On the other hand, information on butterfly biology, in general, permits some conjecture on the types of predators that MNSW potentially face in each life stage, as discussed in chapter 4. Wiesenborn (2010a) identifies the absence of information on predation as a significant gap in knowledge of MNSW ecology.

## Chapter 4 – Habitat Elements

Habitat elements consist of specific habitat conditions that allow or prevent, or promote or inhibit, one or more critical biological activities and processes. This chapter identifies 15 habitat elements that affect one or more critical biological activities and processes, or affect other habitat elements that in turn affect one or more critical biological activities and processes, across the four MNSW life stages. Some of these habitat elements differ in their details among life stages. For example, different MNSW life stages likely experience predation by different species and/or sizes of invertebrates and vertebrates. However, using the same labels for the same *kinds* of habitat elements across all life stages makes it easier to compare and integrate the CEM for each life stages into a single overarching CEM. Table 4 lists the 15 habitat elements and the critical biological activities and processes that they *directly* affect across all MNSW life stages. Four habitat elements affect critical biological activities and processes only indirectly through effects on other habitat elements.

Table 4.—MNSW habitat elements and the critical activities and processes they directly affect

Critical biological activity and process →	Contamination and infection	Feeding/watering	Hiding/resting	Mating	Ovipositing	Physiological stress	Predation
Habitat element ↓							
Chemical contaminants	X						
Competitors			X				
Fire regime							
Infectious agents	X						
Inundation regime		X				X	
Nectar sources		X					
Predators							X
Quailbush litter condition			X	X			
Quailbush patch distribution							
Quailbush patch size and structure		X	X	X	X	X	
Quailbush shrub condition		X	X	X	X	X	X
Scientific study							
Soil moisture							
Soil nitrogen							
Soil salinity							

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

The diagrams and other references to habitat elements elsewhere in this document identify the habitat elements by a one-to-three-word short name. Each short name refers to a longer, complete name. For example, the habitat element label, “scientific study,” is the short name for “The types, frequencies, and duration of scientific observation, capture, and handling of MNSW during field investigations.” The following paragraphs provide the full name and a detailed definition for each habitat element, addressing the elements in alphabetical order.

## **CHEMICAL CONTAMINANTS**

*Full name:* **The concentrations of chemical contaminants in the air, on plant surfaces, and/or on the leaf litter beneath plants at locations with or potentially suitable for MNSW habitat that could harm MNSW or the plant species on which it depends.** This element includes chemicals that may drift in the air or leach into the groundwater to reach MNSW habitat or that may be present at MNSW habitat sites restored from former land uses. In principal, the element includes biocides, fertilizers, and industrial wastes. The literature reviewed and experts consulted to prepare this CEM does not identify any specific chemical contaminants of potential concern for MNSW habitat sites. However, as noted above (chapter 3, “Contamination and Infection”), neonicotinoid pesticides are widely used on alfalfa and cotton, which are both grown extensively on fields surrounding MNSW habitat sites along the LCR. These potent insecticides are known to harm insects feeding on floral nectar in fields to which these pesticides have been applied and can contaminate groundwater as well (Goulson 2013; Cutler et al. 2014; Pecenka and Lundgren 2015). MNSW adults travel outside their natal quailbush habitat sites to feed, including in nearby alfalfa fields (see chapter 3, “Feeding/Watering”) where they could be exposed to these contaminants. The potential also exists for these contaminants to disperse into MNSW habitat sites. Consequently, chemical contamination of MNSW is a theoretical possibility.

## **COMPETITORS**

*Full name:* **The species, spatial and temporal distributions, abundances, and activity levels of invertebrates and vertebrates that compete with MNSW for food materials and/or physical habitat.** Field reports routinely mention the presence of other insects in MNSW habitat (Nelson and Andersen 1999; Nelson and Wydoski 2013), and recent field studies of MNSW habitat maintain records of these observations. Nelson et al. (2015) specifically report that vegetation patches occupied by MNSW are used also by other butterflies, including pygmy blue (*Brephidium exilis*); marine blue (*Leptotes marina*), ceraunus blue (*Hemiargus ceraunus*); Reakirt's blue (*Echinargus Isola*); checkered white

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

(*Pontia protodice*); orange sulfur (*Colias eurytheme*); dainty sulfur (*Nathalis iole*); common checkered-skipper (*Pyrgus communis*); Eufala skipper (*Lerodea eufala*); and fiery skipper (*Hylephila phyleus*). The authors further state, "Some of these species were likely using plot vegetation. Marine, Ceraunus, and Reakirt's blues use mesquite as a larval host plant and a Pygmy blue was observed laying eggs on quail bush seed heads." In addition to these butterflies, Nelson et al. (2015) report that vegetation patches occupied by MNSW are used by "Ensign coccids (?*Orthezia*), aphids (*Aphidoidea*), galls (various insects), grasshoppers (*Orthoptera*), ...and the moth *Trichocosmia inornata*." The field investigators also recorded "egg-laying damage caused by cicadas (*Diceroprocta apache*)" and noted significant damage to quailbush health by ensign coccids at one site. MNSW thus may face a wide range of insect competitors for nectar sources and for quailbush shrubs as habitat and food resource.

MNSW may also face competition from vertebrates that feed on quailbush leaves or seeds. Meyer (2005) notes that mule deer, pronghorn, rabbits, rodents, and goats and other livestock browse the leaves, and deer mice eat the seeds, although not as a first choice. Nectar-source species presumably attract their own spectra of browsers and seed eaters as well.

## **FIRE REGIME**

**Full name: The frequency, timing, spatial extent, and intensity of fire at locations with or potentially suitable for MNSW habitat.** Wildfire is a natural type of disturbance in the riparian plant communities of the LCR, and wildfires today also occur through human accidents (MacNally et al. 2004; Meyer 2005; Conway et al. 2010; Reclamation 2013, 2014). Under the LCR MSCP, prescribed fire is used as a tool for habitat management (Reclamation 2014).

Fire is lethal to MNSW but has varying effects on their nectar sources and host plants. In a lengthy review of quailbush ecology, Meyer (2005) notes that the high moisture, salt, and ash content of individual quailbush plants reduces their flammability (increases their fire resistance) compared to other desert shrubs, that quailbush can survive some fires and can regenerate from adventitious buds following fire, and that quailbush can rapidly recolonize burn sites through onsite and offsite seed production and dispersal. Otherwise, Meyer (2005) notes no specific adaptations of quailbush to fire and suggests that quailbush habitat does not burn often (35- to 100-year return interval) under natural conditions; he also notes a lack of research on the fire ecology of the species.

Fire resistance and/or adaptations vary among MNSW nectar sources (see chapter 3, table 3, for a list of nectar sources). Saltcedar is highly fire adapted: the high moisture content of its leaves make them poorly flammable, and plants can regenerate from root crowns even following top-kill from a fire (Zouhar 2003;

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Nagler et al. 2011). However, its leaf and branch litter are highly flammable and, in dense thickets, may result in a greater frequency of fires, and in fires of high severity, that destroy even some root crowns (Zouhar 2003). Mesquite, on the other hand, is not fire resistant (Ohmart et al. 1988; Nagler et al. 2011). Among the other nectar sources, only arrowweed, a shrub, resembles saltcedar in being both halophytic and fire resistant (Zouhar 2003). Sweetbush, another shrub, appears able to recover from roots and/or seeds following fire (Brown and Minnich 1986). Salt heliotrope, western purslane, alkali mallow, and common purslane are all native perennial herbs adapted to the natural fire regimes of the plant communities in which quailbush occurs (Meyer 2005). They are readily destroyed by fire but able to recolonize burned sites rapidly through seed dispersal from surrounding areas.

## **INFECTIOUS AGENTS**

*Full name:* **The species, abundances, spatial and temporal distributions, and activity levels of infectious agents to which MNSW are susceptible at locations with or potentially suitable for MNSW habitat.** As noted above (see chapter 3, “Contamination and Infection”), MNSW in every life stage presumably are vulnerable to infection, as are all butterflies (Altizer and de Roode 2010). Non-lethal infections may make the affected individuals vulnerable to mortality from other causes. “Infectious agents” refers to viruses, bacteria, fungi, and parasites present and capable of infecting MNSW in the open environment of the LCR valley. The literature reviewed for this CEM does not identify any specific infectious agents known or suspected to affect MNSW.

## **INUNDATION REGIME**

*Full name:* **The frequency, timing, spatial extent, and duration of inundation at locations with or potentially suitable for MNSW habitat.** Inundation by floodwaters from the Colorado River and/or its tributaries was a natural and ecologically important type of disturbance affecting the riparian vegetation of the LCR valley prior to river regulation (Ohmart et al. 1988; Stromberg et al. 2007). Due to river regulation, uncontrolled flooding no longer occurs. However, MNSW habitat under LCR MSCP management may be subject to flooding in the course of site management (Reclamation 2014). This habitat element refers only to inundation, not high-energy flooding that could scour MNSW habitat: MNSW habitat sites along the LCR valley no longer experience such scouring as a consequence of river regulation.

Inundation presumably could drown MNSW pupae in the leaf litter below quailbush shrubs and could also drown eggs and larvae on lower shrub branches

depending on flood depth. Flooding also can displace or remove leaf litter. On the other hand, quailbush occur primarily in riparian and other settings that experience occasional flooding (Meyer 2005). Saline soils are the other major determinant of quailbush patch distribution (Meyer 2005). Quailbush can tolerate flooding and have been observed to survive flooding for most of a growing season and even experience some root growth while inundated (Meyer 2005). Saltcedar, mesquite, and arrowweed are also flood tolerant, although mesquite are more susceptible to drowning than are either saltcedar or arrowweed (Reclamation 1995). The herbaceous nectar source species may tolerate seasonal inundation to varying degrees, but the literature reviewed for this CEM did not include information on this aspect of their ecology. Quailbush and MNSW nectar sources, all adapted to desert riparian settings, presumably can recover quickly following flood disturbance, creating or re-establishing habitat conditions favorable to MNSW persistence or recolonization.

## **NECTAR SOURCES**

***Full name:* The species, visibilities, size ranges, spatial and temporal distributions, abundances, and nectar abundance and nutritional quality of plants that MNSW may use as nectar sources at locations with, accessible to, or potentially suitable for MNSW habitat.** Nelson and Andersen (1999) note that “[a]ppropriate quantity and quality of nectar can increase fecundity, larval fitness, and adult longevity of some butterflies, all attributes potentially important for colony persistence.” Table 3 (see chapter 3, “Feeding/Watering”) lists the plant species known or suspected to serve as floral or extrafloral nectar sources for MNSW adults. As also noted above (see chapter 3, “Feeding/Watering”), MNSW females ingest significant quantities of nectar, preferentially select flowers with higher nectar sugar content, and spend more time feeding when flowers have lower sugar content (Wiesenborn 2010a, 2011; Wiesenborn and Pratt 2010). In contrast, MNSW males do not ingest significant quantities of nectar nor select flowers with higher nectar sugar content and do not spend more or less time feeding when flowers have lower sugar content (Wiesenborn 2010a, 2011; Wiesenborn and Pratt 2010).

MNSW appear to identify potential flora nectar sources based on the visible color reflectance of flowers observed during flight but appear to land preferentially on flowers based on ultraviolet light absorbance (Pratt and Wiesenborn 2009; Reclamation 2009; Wiesenborn 2010b). They also prefer flowers in open sun rather than in shade (Wiesenborn and Pratt 2010). They prefer flowers in the yellow-to-purple visible color reflectance range of salt heliotrope flowers, the most common and most frequently selected of native floral nectar sources (Pratt and Wiesenborn 2009; Reclamation 2009; Wiesenborn 2010a, 2010b, 2011). Heliotrope flower centers are yellow when young, turning purple with age (Wiesenborn 2011). The amount of nectar and sugar mass in heliotrope flowers decline as the flowers age and turn color from yellow- to purple-centered along a

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

cyme, although purple-centered flowers generally outnumber the yellow-centered ones as a cyme ages (Wiesenborn 2011). MNSW also feed on native flowers with pink and magenta reflectance. They do not appear to use olfactory cues to identify potential nectar sources while flying or when landing (Wiesenborn 2010a, 2010b). The literature reviewed for this CEM does not suggest how MNSW adults find extrafloral nectar sources.

Wiesenborn and Pratt (2010), in their study of MNSW preferences among floral nectar sources, reported nectar sugar content as “sugar mass,” calculated by converting actual sugar concentration (milligrams per liter [mg/L]) to milligrams (mg) of sugar based on the 5-milliliter inflorescence-rinse volume. They found that females selected nectar sources with sugar masses of  $0.30 \pm 0.07$  mg (males:  $0.13 \pm 0.02$  mg). The authors also suggest that MNSW females – like other butterflies described in the literature – may prefer nectar with higher concentrations of amino acids (see also Pratt and Wiesenborn 2009; Wiesenborn 2010a; Nelson et al. 2015). Nelson et al. (2015) specifically suggest that females may seek nectar richer in amino acids if their natal quailbush provided them (as larvae) with leaves of lower nutritional quality.

The abundance of different nectar sources varies over time within a year: different nectar source species flower at different times of the year, between spring and autumn, and at different times of the day (Nelson and Andersen 1999; Pratt and Wiesenborn 2009). The different nectar source species also differ in their availability under different weather conditions: heliotrope can dry up entirely under very dry conditions (Wiesenborn 2010a, 2010b); in contrast, alfalfa can produce more blooms with more nectar immediately following significant rainfall and thereby attract MNSW even across moderate distances (Reclamation 2013). The discussions of fire regime, inundation regime, soil moisture, soil nitrogen, and soil salinity, this chapter, provide additional information on factors affecting nectar source diversity, abundance, and condition.

## **PREDATORS**

*Full name:* **The species, spatial and temporal distributions, abundances, and activity levels of invertebrates and vertebrates that prey on MNSW at locations with or potentially suitable for MNSW habitat.** The literature reviewed and experts consulted to prepare this CEM do not identify any particular species that may prey on MNSW of any life stage. As noted earlier, Wiesenborn (2010a) identifies the absence of information on predation as a significant gap in knowledge of MNSW ecology.

Richard Wydoski, a Reclamation biologist (2015, personal communication), suggests native praying mantises (insects of the Order, Mantodea) and spiders as possible types of invertebrate predators on MNSW in the LCR valley. Mantises would hunt in the foliage, while spiders would be expected to hunt and trap both

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

within the foliage and within the leaf litter beneath quailbush shrubs. Dragonflies (Odonata) are another large class of potential invertebrate predators known to prey on and thereby significantly affect the abundance and diversity of butterflies (Tiitsaar et al. 2013).

Butterflies, in general, are also at risk from predation by insectivorous birds overhead and by ground-based insectivorous birds and mammals. MNSW pupae and larvae on low-lying branches would be particularly vulnerable to ground-based predators. Meyer (2005) notes that, because of their high arthropod densities and dense cover, quailbush shrubs in fact attract a wide range of insectivorous birds.

Anderson (2012) summarizes data on avian feeding on insects along the LCR valley from 1976–80, quantifying what species of insects each species of bird consumed. Anderson (2012) reports the results by season, indicating for each bird species the proportion of individual insects it consumed from each taxonomic order of insect. Table 4 summarizes the results from Anderson (2012) for the 23 species of birds for which Lepidoptera comprised an average of at least 1 percent of their diet during one or more seasons.

Table 5.—Proportion of Lepidoptera in diets of insectivorous birds along the LCR valley, 1976–80, by season (after Anderson 2012)

Bird species	Winter	Spring	Summer	Late summer
<i>Mimus polyglottos</i> , northern mockingbird				40.65
<i>Icterus bullockii</i> , Bullock's oriole		47.6	30.2	
<i>Oreothlypis luciae</i> , Lucy's warbler		43.4	22.8	
<i>Auriparus flaviceps</i> , verdin	20.7	34	55.1	18.38
<i>Myiarchus cinerascens</i> , ash-throated flycatcher		39	14.1	
<i>Toxostoma crissale</i> , Crissal thrasher	23.2	23.5	18.4	40
<i>Melospiza aberti</i> , Abert's towhee	27	38.2	15.5	20.4
<i>Campylorhynchus brunneicapillus</i> , cactus wren			19.6	
<i>Phainopepla nitens</i> , Phainopepla			16.7	
<i>Setophaga coronata</i> , yellow-rumped warbler	9.3	9.7		30.14
<i>Polioptila melanura</i> , black-tailed gnatcatcher	8.3	16	22	15.29
<i>Oreothlypis celata</i> , orange-crowned warbler	3.5			18.87
<i>Catharus guttatus</i> , hermit thrush	10.4			
<i>Melospiza melodia</i> , song sparrow			9.7	
<i>Polioptila caerulea</i> , blue-grey gnatcatcher	8.8			
<i>Passerina caerulea</i> , blue grosbeak			8.6	
<i>Dryobates scalaris</i> , ladder-backed woodpecker		8.2		
<i>Callipepla gambelii</i> , Gambel's quail				7.15
<i>Chordeiles acutipennis</i> , lesser nighthawk			6.8	
<i>Tyrannus verticalis</i> , western kingbird			6.2	
<i>Coccyzus americanus</i> , yellow-billed cuckoo			6.1	
<i>Zonotrichia leucophrys</i> , white-crowned sparrow				5.08
<i>Regulus calendula</i> , ruby-crowned kinglet	0.9			2.91

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

The data tables in Anderson (2012) do not indicate consumption frequencies for individual species of Lepidoptera, such as MNSW. However, the avian species observed consuming Lepidoptera include some that feed aerially and many that forage beneath and within the foliage of shrubs. Meyer (2005), for example, notes that Gambel's quail (*Callipepla gambelii*) specifically uses quailbush shrubs as cover and ground-level feeding habitat. Anderson (2012) also notes that the birds he studied consumed not only butterfly and moth adults but also caterpillars and pupae. MNSW thus may face a wide array of avian predators during every life stage.

## **QUAILBUSH LITTER CONDITION**

*Full name:* **The thickness, moisture level, density, spatial extent, and stability of leaf and twig litter beneath individual quailbush shrubs at locations with or potentially suitable for MNSW habitat.** This element refers to the dead, decomposing leaves and twigs that accumulate beneath individual quailbush shrubs (Meyer 2005). MNSW larvae may overwinter in this litter, MNSW pupate within the litter (see chapters 2 and 3), and some predators on MNSW may live or at least forage within the litter (see "Predators," above). The literature reviewed to prepare this CEM does not identify specific ways in which the thickness, moisture level, density, spatial extent, and stability of the litter beneath individual shrubs are known or suspected to affect MNSW pupation or foraging by predators within the litter. Nevertheless, it is plausible that such relationships exist. For example, dense litter could reduce foraging efficiency by the partly insectivorous Gambel's quail, which uses quailbush patches as cover and feeding habitat. Dense litter may also provide fuel for wildfire (Meyer 2005; Conway et al. 2010).

## **QUAILBUSH PATCH DISTRIBUTION**

*Full name:* **The sizes, numbers, and proximity of quailbush patches to each other across the landscape.** This element refers to the capacity of the LCR landscape to support MNSW through the presence of quailbush patches of sufficient sizes, numbers, and proximity to each other. It is not known how quailbush patches were distributed or shifted over time prior to river regulation and alteration of the LCR flood plain. However, quailbush patches develop opportunistically following disturbance in flood plains with riparian vegetation (Meyer 2005; Pratt and Wiesenborn 2011). Consequently, the historic flood plain of the LCR likely contained large numbers of quailbush patches throughout the riparian corridor (Ohmart et al. 1988; Nelson and Andersen 1999). MNSW nevertheless may not always have dispersed readily in the historic landscape. Nelson and Andersen (1999) cite a study finding that "... some [butterfly] taxa may take 2–3 years to colonize patches just 300–700 m from source populations."

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

The largest distance reported in the literature, across which MNSW have been observed to fly and return, is approximately 0.25 kilometer from a study site to a field of sweetbush (Wiesenborn 1997) (see chapter 3, “Feeding/Watering”). Richard Wydoski, a Reclamation biologist (2015, personal communication), suggests that MNSW adults may be able to disperse most easily across distances of 100 m or less.

Nelson and Andersen (1999) and Nelson et al. (2014) note an absence of data on quailbush dispersal distances or minimum suitable quailbush patch sizes in MNSW studies. Nelson and Andersen (1999) and Pratt and Wiesenborn (2011) note that quailbush patches are highly discontinuously distributed across the present-day LCR flood plain. River regulation and land development have inundated natural riparian terrain and removed riparian vegetation from other flood plain terrain, creating large gaps in the distribution of quailbush patches. Saltcedar also can outcompete quailbush for habitat space (Pratt and Wiesenborn 2011). For example, Pratt and Wiesenborn (2011) identified three pairs of quailbush sites along the LCR valley occupied by MNSW but separated by distances of 30, 65, and 160 kilometers, respectively, in which only one small, unoccupied quailbush patch (1 pair) or no quailbush patches (2 pairs) were present. The authors suggest that the lack of quailbush patches across such large distances presents a significant barrier to MNSW dispersal.

## **QUAILBUSH PATCH SIZE AND STRUCTURE**

*Full name:* **The overall size, density, canopy height, percent cover, patchiness of cover, and range of ages and sizes among quailbush plants within individual quailbush patches.** MNSW habitat patches consist of areas of vegetation dominated by quailbush with adjacent or inter-mixed nectar sources, surrounded by areas lacking such vegetation. Pratt and Wiesenborn (2009) collected data from multiple transects through vegetation “patches” at a site occupied by MNSW. Vegetation cover in the patches consisted of 37–76 percent quailbush followed by honey mesquite, alkali mallow, desertbroom baccharis (*Baccharis sarothroides*), saltcedar, and arrowweed. Nectar sources comprised an average of 3 percent of the cover and included salt heliotrope and western purslane (see “Feeding/ Watering,” above).’

However, Pratt and Wiesenborn (2009) did not record their criteria for defining a “patch.” Nelson et al. (2015) similarly do not define what constitutes a “patch” of MNSW habitat but note that such patches may consist of a cluster, band, or linear strip of vegetation. Pratt and Wiesenborn (2011) observed that MNSW could be found in patches consisting of “fewer than half a dozen” quailbush shrubs so long as the shrubs were suitably lush (see chapter 4). In turn, Nelson et al. (2014) noted that MNSW at the CVCA occupied an area of only “10’s of square meters” that nevertheless provided suitable adult nectar and larval host plant resources to

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

function as a habitat patch. On the other hand, Nelson et al. (2014) caution that this observation may underestimate the actual patch size at the CVCA due to the difficulty of detecting MNSW in the field. Wiesenborn (2010a) in fact cites a study finding that butterflies, in general, require habitat patches of 2–6 hectares to persist. In light of these uncertainties, Nelson et al. (2014, 2015) suggest a need for a clearer understanding of minimum MNSW habitat patch size.

The amount of shading present within an individual quailbush patch does not correlate simply with plant canopy size among sites because shading also depends on shrub lushness and on the presence/absence of other shading vegetation such as trees (Wiesenborn 1997; Pratt and Weisenborn 2011; Nelson et al. 2014). However, the amount of shade presumably increases with increasing canopy height among plants of similar lushness.

As noted earlier, MNSW adults reportedly can easily traverse distances of approximately 4 m between individual quailbush shrubs (Wiesenborn 1997). However, the literature reviewed for this CEM does not specifically address whether quailbush shrub spacing affects MNSW behaviors or habitat selection.

## **QUAILBUSH SHRUB CONDITION**

***Full name:* The age, height, and diameter of individual quailbush shrubs and the leaf size, water content, and nutritional quality for individual shrubs at locations with or potentially suitable for MNSW habitat.** Quailbush leaves provide MNSW larvae with food, water, shade, and shelter, and the overall shrubs provide them with shelter and with pupation sites either within the foliage or in the litter below (see chapter 3, “Hiding/Resting”). In turn, quailbush shrubs provide MNSW adults with shade and shelter from predators and with resting sites that may provide wide fields of vision (see chapter 3, “Hiding/Resting”). Presumably, quailbush plants with more abundant and lush foliage provide greater shading and shelter (Nelson et al. 2014, 2015).

As discussed above (see chapter 3, “Ovipositing”), MNSW females select quailbush plants for ovipositing based on a very specific set of criteria concerning shrub condition: canopy diameter > 1.6 m; leaf-water content > 64 percent; and leaf-nitrogen content (dry weight of total Kjeldahl nitrogen as percent of dry leaf weight) > 3.2 percent (Wiesenborn and Pratt 2008; Reclamation 2009). The minimum number of eggs deposited on a plant increases with increasing canopy diameter, leaf moisture, and/or leaf nitrogen above these threshold values, but the maximum number of eggs does not. MNSW sometimes do oviposit on plants that do not meet all three criteria but with decreasing probability among plants with smaller canopies, lower leaf-water content, and/or lower leaf-nitrogen content. However, MNSW do not appear to oviposit on plants with canopy diameter < 1.0 m and/or leaf-nitrogen content < 2 percent (Wiesenborn and Pratt 2008).

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

For example, they will oviposit on smaller shrubs (“seedlings”) when larger plants are not available but only if the shrubs provide suitable levels of leaf-water and/or leaf-nitrogen content (Nelson et al. 2014).

This pattern of selectivity among MNSW females for where to lay their eggs presumably results in eggs being laid on plants that provide the best habitat for larval development. As noted above (see chapter 3, “Feeding/Watering”), MNSW larvae reportedly survive and develop best when on leaves with a leaf-water content > 64 percent and a leaf-nitrogen content > 3.2 percent (Wiesenborn and Pratt 2008; Reclamation 2009, 2013; Nelson et al. 2015).

As also noted above (see chapter 3, “Ovipositing”), MNSW females likely identify plants suitable for ovipositing based on visual cues such as the greenness of a plant, an indicator of leaf-nitrogen content (Wiesenborn and Pratt 2008; Nelson et al. 2015). Ongoing LCR MSCP studies are being conducted to test the feasibility of measuring leaf greenness as a way to quantify this indicator (S.M. Nelson 2015, personal communications). The proportion of dry leaves on a quailbush shrub likely provides another visual cue concerning shrub condition: Nelson et al. (2015) report that, with a very high statistical significance, females simply do not lay eggs on plants with more than a small percentage of dry leaves present.

It is not clear why MNSW females select quailbush shrubs with large canopy diameters for ovipositing. Wiesenborn and Pratt (2008) suggest that MNSW females preferentially oviposit on plants with larger diameters simply because such plants provide more shade, which helps MNSW control their body temperature (Wiesenborn 1999). Two other pieces of information support this suggestion. First, MNSW females appear to oviposit preferentially on quailbush growing in the shade of trees (Pratt and Wiesenborn 2011). Second, MNSW females oviposit more frequently during the morning and early afternoon (Pratt and Wiesenborn 2009), a window of time that avoids the highest air temperatures of the day.

## **SCIENTIFIC STUDY**

*Full name:* **The types, frequencies, and duration of scientific observation, capture, and handling of MNSW during field investigations.** Publications on field studies of MNSW routinely remark on the difficulty of observing the butterflies (Pratt and Wiesenborn 2009; Nelson et al. 2014, 2015), resulting from the MNSW adult preference for flying mostly within the canopy of quailbush shrubs. As a result, field protocols have been developed that are designed to improve observation of this challenging species and the testing of increasingly complex field methods to assess MNSW occupancy, such as the use of environmental deoxyribonucleic acid (eDNA) (Nelson et al. 2015).

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Conversely, some field methods may cause harm to MNSW. Nelson et al. (2015) describe and cite a supporting study that field methods such as capture, mark, and re-capture techniques can have “adverse effects” on butterflies, particularly on small-winged species such as MNSW. Consequently, recent field monitoring of the MNSW population status (Nelson et al. 2015) has resulted in the collection of only presence/absence data using only minimally intrusive methods of observation. Otherwise, the literature reviewed to prepare this CEM does not provide information on potential effects of scientific study on MNSW. Pratt and Wiesenborn report several studies involving handling of MNSW in the laboratory or the field but do not report any resulting harm to either adults or larvae (Wiesenborn 1999; Pratt and Wiesenborn 2009). This absence of reports of harm is consistent with Willis et al. (2009), who report on the results of an experiment in artificial relocation (assisted colonization) with two skipper species in the United Kingdom. The authors note that skippers were netted, caged, transported, and released with no reported harm.

## **SOIL MOISTURE**

*Full name:* **The moisture of the soils at locations with or potentially suitable for MNSW habitat.** This element refers to the degree (e.g., percent) of saturation of a soil with water. Fully saturated soils, such as those with standing surface water, are said to have 100 percent soil moisture. Soil moisture appears to affect MNSW indirectly by affecting the leaf-water and leaf-nitrogen content of quailbush (Wiesenborn and Pratt 2008; Pratt and Wiesenborn 2011; Wiesenborn 2012a; Nelson et al. 2014, 2015). Soil moisture levels below 10 percent result in dry leaves and leaf loss in quailbush, and the plants respond poorly to soil saturation (waterlogging) as well (Nelson et al. 2014, 2015). Soil moisture in the range of 50–70 percent appears to result in the most attractive levels of leaf-water and leaf-nitrogen content for MNSW plant selection (Nelson et al. 2014, 2015). Through ongoing LCR MSCP studies, data have been collected, but analyses have not been completed, on how leaf-water content, leaf-nitrogen content, soil moisture, and MNSW usage rates vary continuously relative to each other. However, Nelson et al. (2015) note that measurements of soil moisture beneath quailbush shrubs used versus not used by MNSW have wide variances and can be affected by recent rainfall events, the effects of which on the plants may take time to emerge. Consequently, it is not yet possible to identify an optimal range of soil moistures for purposes of soil management to benefit quailbush and MNSW abundances. Nevertheless, observations over many years indicate a general pattern: (1) quailbush shrubs exhibit greater lushness in areas of moderate (but not excessive) soil moisture, including following rainfall, but (2) the timing of when soil moisture levels result in lush quailbush foliage may not coincide with MNSW needs (Wiesenborn and Pratt 2008; Wiesenborn 2012a; Nelson et al. 2014, 2015).

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

As noted earlier (see “Nectar Sources,” above), soil moisture conditions affect the availability, quality, and spatial distribution of nectar sources. For example, heliotrope can dry up entirely under very dry conditions (Wiesenborn 2012b). In contrast, alfalfa can produce more blooms with more nectar immediately following significant rainfall and thereby attract MNSW even across moderate distances (Reclamation 2013). However, the literature reviewed for this CEM does not systematically address the ways in which soil moisture may affect nectar source density or the masses or quality of the nectar they produce.

## **SOIL NITROGEN**

*Full name:* **The concentrations of biologically available nitrogen in the soils at locations with or potentially suitable for MNSW habitat.** Quailbush also fix nitrogen from the atmosphere through root-symbiotic bacteria (Wiesenborn and Pratt 2008). Some of the literature reviewed for this CEM also suggests that low levels of soil nitrogen availability could result in low leaf-nitrogen content in quailbush leaves, a situation that could be managed through the addition of soil fertilizers (Reclamation 2009; Wiesenborn 2010a). However, the literature reviewed for this CEM provides no data on soil nitrogen content in quailbush locations or on how leaf-nitrogen content varies with soil nitrogen content.

On the other hand, the plants that provide nectar to MNSW likely do respond to variation in soil nitrogen availability. That is, soil nitrogen conditions likely also affect nectar source spatial distributions, density and/or the masses, or quality of the nectar they produce. However, the literature reviewed for this CEM does not systematically address this topic. Marler et al. (2001) found that saltcedar produces more stems and achieves higher shoot biomass, total biomass, and shoot:root biomass ratio values with increasing soil nitrogen availability in applications of mixed N- and P-fertilizers. In contrast, the review of saltcedar ecology by Zouhar (2003) makes no mention of the sensitivity of saltcedar to soil nitrogen levels. Honey mesquite fixes nitrogen (Bailey 1976) and, as with quailbush, its condition therefore may not be sensitive to soil nitrogen levels. The literature reviewed for this CEM otherwise does not address the effects of soil nitrogen levels on MNSW nectar sources.

## **SOIL SALINITY**

*Full name:* **The salinity of the soils at locations with or potentially suitable for MNSW habitat.** Soil salinity affects MNSW indirectly through its effects on quailbush. Quailbush tolerate relatively high levels of soil salinity and can germinate in soils with salinities as high as 18,000 mg/L, although they grow better in soils with salinities below 6,000 mg/L (Meyer 2005). Quailbush uptake

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

of cations such as sodium, calcium, and potassium varies with soil salinity (Meyer 2005). Quailbush tolerance of high soil salinity gives it a competitive advantage over many other desert riparian plants but not over saltcedar (Nagler et al. 2011; Pratt and Wiesenborn 2011). None of the publications reviewed for this CEM provide information on whether soil salinity affects quailbush biology in any ways that in turn affect MNSW use of the plants.

Soil salinity also may affect MNSW directly through its effects on the water in puddles from which MNSW might seek to drink. However, as noted above (see chapter 3, "Feeding/Watering"), MNSW adults appear to obtain most or all of their water from nectar. The field studies conducted along the LCR reviewed for this CEM resulted in no evidence of puddling by MNSW adults despite the apparent presence of opportunities for such behavior (Pratt and Wiesenborn 2009; Nelson et al. 2015). The lack of evidence of puddling may relate to soil salinity, which in turn affects the chemistry of any puddles that may form (Pratt and Wiesenborn 2009).

Soil salinity likely also affects nectar source spatial distributions, density and/or the masses, or quality of the nectar they produce. However, the literature reviewed for this CEM does not systematically address this topic.

## 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. They may also significantly directly affect some critical biological activities and processes. A hierarchy of such factors exists, with long-term dynamics of climate and geology at the top. However, this CEM focuses on six immediate controlling factors that lie within the scope of potential human manipulation. The six 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 6 lists the six controlling factors and the habitat elements they *directly* affect.

Table 6.—MNSW controlling factors and the habitat elements they directly affect

Affected habitat element →	Chemical contaminants	Competitors	Fire regime	Infectious agents	Inundation regime	Nectar sources	Predators	Quailbush litter condition	Quailbush patch distribution	Quailbush patch size and structure	Quailbush shrub condition	Scientific study	Soil moisture	Soil nitrogen	Soil salinity
Causal controlling factor ↓															
Offsite land management and use	X	X		X	X	X			X	X			X		
Onsite fire management			X												
Onsite vegetation management	X		X			X	X			X	X	X		X	
Onsite visitation and study		X		X			X					X			
Onsite water management			X		X							X	X		X
Reach-scale water management					X										

The diagrams and other references to controlling factors elsewhere in this document identify the controlling factors by a one-to-three-word short name. Each short name refers to a longer, complete name. For example, the controlling factor label, “onsite fire management,” is the short name for “The types, frequencies, and duration of official activities intended to control and/or suppress fire.” The following paragraphs provide the full name and a detailed definition for each controlling factor, addressing the elements in alphabetical order.

## OFFSITE LAND MANAGEMENT AND USE

**Full name:** The types of land management and land use activities that take place on lands that surround existing or potential MNSW habitat sites.

Lands under the mandate of the HCP that contain MNSW habitat and potential habitat are surrounded by lands used for a variety of purposes, including other LCR MSCP activities, irrigation farming, rangeland, and recreation. Landowners include Reclamation, private individuals, Nevada Department of Wildlife, Fort Mojave Indian Tribe, National Park Service, U.S. Fish and Wildlife Service, and the Bureau of Land Management (Pratt and Wiesenborn 2011).

Activities taking place on these surrounding lands that could affect MNSW or their habitat include (Reclamation 2004; Nelson and Wydoski 2013):

- Irrigation and the operation of irrigation water deliveries, return flows, and groundwater elevations.
- Planting of crops and management of ground cover, including around agricultural field margins.
- Management activities to control or remove nuisance species, including aerial spraying of biocides for crop management (see chapter 4, “Chemical Contaminants”).
- Fire management, including wildfire suppression, prescribed fire, and management of fire control barriers.
- Control and removal of the invasive saltcedar, aka tamarisk. Saltcedar aggressively competes with quailbush and nectar sources such as the honey mesquite for space and soil moisture (see chapter 4, “Competitors,” and “Soil Moisture”) but also can serve as a nectar source for MNSW (see chapter 4, “Nectar Sources”) and a source of shade for quailbush patches (see chapter 4, “Quailbush Patch Size and Structure”). Resource managers in the Upper Colorado River Basin released tamarisk leaf beetles (*Diorhabda carinulata*) to defoliate and thereby eliminate or control the distribution of tamarisk. The unintended spread of these beetles into the LCR valley (Nelson and Wydoski 2013; Reclamation 2014) has the potential to significantly alter the interactions of tamarisk with MNSW, its host plant, and its nectar sources (see chapter 4, “Competitors,” “Nectar Sources,” “Quailbush Patch Distribution,” “Quailbush Patch Size and Structure,” and “Soil Moisture”).

## ONSITE FIRE MANAGEMENT

*Full name:* **The types, frequencies, and duration of official activities intended to control and/or suppress fire.** Under the LCR MSCP, prescribed fire is used as a management tool as is actively managing wildfires through fire suppression and the construction of fire control breaks (Nelson and Wydoski 2013; Reclamation 2013, 2014).

## ONSITE VEGETATION MANAGEMENT

*Full name:* **The types, frequencies, and duration of official activities intended to manage the taxa, abundances, conditions, and spatial distributions of vegetation on sites managed to support MNSW habitat.** Under the LCR MSCP, a range of methods is used in addition to prescribed fire to manage vegetation on lands under its authority, including surface irrigation and subirrigation, planting, fertilizing, thinning and hand removal, discing and plowing, and the application of herbicides (Reclamation 2014). Reclamation may also remove vegetation as part of management actions to maintain roads and canals on its lands, and this can result in the removal of linear patches of quailbush and nectar sources for MNSW (Wiesenborn 2010a).

## ONSITE VISITATION AND STUDY

*Full name:* **The types, frequencies, and durations of scientific activities at sites under study as existing or potential MNSW habitat and the types, frequencies, durations, and purposes of other visits to the sites.** LCR MSCP biologists routinely visit sites with and without MNSW to assess species abundance, test new field methods, and assess the relationships among factors that may affect MNSW abundance (Nelson et al. 2014, 2015). Scientists from other institutions have also carried out studies of MNSW abundance and habitat selection (Wiesenborn and Pratt 2008, 2010; Pratt and Wiesenborn 2009, 2011). Sites occupied by MNSW or potentially suitable as MNSW habitat also occur in areas visited by other Reclamation resource managers ( Reclamation 2013, 2014). Additionally, MNSW habitat and sites potentially suitable as MNSW habitat occur within the Cibola National Wildlife Refuge, managed by the U.S. Fish and Wildlife Service (see chapters 3 and 4). Visitation to the refuge therefore could result in visitation to the CVCA and its MNSW habitat sites.

## ONSITE WATER MANAGEMENT

*Full name:* **The types, frequencies, and durations of official activities that affect the delivery and distribution of regulated water within sites managed to support MNSW habitat.** Under the LCR MSCP, sites with MNSW habitat are actively irrigated as are potential habitats at the Palo Valley Ecological Reserve and CVCA habitat management sites (Nelson et al. 2014). Locations within both sites have been managed using floor irrigation at various times in their management histories, and CVCA managers also have irrigated 2-foot-deep furrows to create linear habitat patches for MNSW (Reclamation 2009, 2012; Wiesenborn 2010a, 2011, 2012a, 2012b; Nelson et al. 2014, 2015). MNSW occupy patches at the Hart Mine site adjacent to a marsh that maintains high groundwater elevations in its vicinity as a result of LCR MSCP management of marsh water levels (Nelson et al. 2015). Irrigation water also unintentionally supports quailbush and nectar sources for MNSW at the CVCA along ditches that receive water from leaking flood irrigation gates (Reclamation 2012; Nelson et al. 2015). Nelson et al. (2014) (see also Nelson et al. 2015) report that flood irrigation has diminished at the CVCA “in recent years,” apparently due to limitations on the availability of water under Reclamation’s water rights.

## REACH-SCALE WATER MANAGEMENT

*Full name:* **The types, frequencies, and durations of official activities that affect the elevation of surface water along the Colorado River and its tributaries along the LCR valley.** The Colorado River through the LCR valley consists of a chain of reservoirs separated by flowing reaches. The water moving through this system is highly regulated for storage and delivery to numerous international, Federal, State, Tribal, municipal, and agricultural users as well as for hydropower generation. This system of water management and its infrastructure comprises almost the only factor affecting surface water elevations along the river (Reclamation 2004). Permanent inundation of the flood plain by reservoirs and entrenchment of the river along flowing reaches have eliminated almost all opportunities for the river to deliver pulses of water onto its former flood plain and have altered water table elevations throughout the valley. These changes have eliminated hydrologic dynamics that previously maintained a diversity of habitat opportunities for quailbush and MNSW along the valley (Nelson and Andersen 1999). At the same time, Reclamation has rights to some of the water in the river that allow for the use of that water on LCR MSCP lands (Nelson et al. 2014; Reclamation 2014).

## Chapter 6 – Conceptual Ecological Model by Life Stage

This chapter contains seven sections. The first section summarizes the methodology used to assess the individual causal links in the CEM for each life stage (see chapter 1 and attachment 1). The second section presents causal relationships common to the CEMs for all four MNSW life stages. These causal relationships concern the ecology of quailbush, the host plant for all four life stages, specifically the causal relationships that shape four habitat elements: quailbush litter condition, quailbush patch distribution, quailbush patch size and structure, and quailbush shrub condition. The third, fourth, and fifth sections present the CEM for the egg, larval, and pupal life stages, respectively. For each life stage, the text and diagrams identify its life-stage outcomes; its critical biological activities and processes; the habitat elements that support or limit the success of its critical activities and processes; the controlling factors that determine the abundance, distribution, and other important qualities of these habitat elements; and the causal links among them. The sixth section presents the causal relationships that affect the ecology of the nectar sources on which adult MNSW depend. Finally, the last section presents the CEM for the adult life stage itself, including its relationships to quailbush and nectar source ecology.

### METHODOLOGY

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

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

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

- **Magnitude** refers to "... the degree to which a linkage controls the outcome *relative to other drivers*" (DiGennaro et al. 2012). Magnitude takes into account the spatial and temporal scale of the causal relationship as well as the strength (intensity) of the relationship at any single place and time. The present methodology separately rates the intensity, spatial scale, and temporal scale of each link on a three-part scale from "Low" to "High" and assesses overall link magnitude by averaging the ratings for these three. If it is not possible to estimate the intensity, spatial scale, or temporal scale of a link, the subattribute is rated as "Unknown" and ignored in the averaging. If all three subattributes are "Unknown," however, the overall link magnitude is rated as "Unknown." Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link magnitude provide information analogous to the size of a correlation coefficient.
- **Predictability** refers to "... the degree to which current understanding of the system can be used to predict the role of the driver in influencing the outcome. Predictability ... captures variability... [and recognizes that] effects may vary so much that properly measuring and statistically characterizing inputs to the model are difficult" (DiGennaro et al. 2012). A causal relationship may be unpredictable because of natural variability in the system or because its effects depend on the interaction of other factors with independent sources for their own variability. Just as the terms for link character provide information analogous to the sign of a correlation coefficient, the terms for link predictability provide information analogous to the size of the range of error for a correlation coefficient. The present methodology rates the predictability of each link on a three-part scale from "Low" to "High." If it is not possible to rate predictability due to a lack of information, the link is given a rating of "Unknown" for predictability.
- **Scientific understanding** refers to the degree of agreement represented in the scientific literature and among experts in understanding how each causal relationship works—its character, magnitude, and predictability. Link predictability and understanding are independent attributes. A link may be highly predictable but poorly understood or poorly predictable but well understood. The present methodology rates the state of scientific understanding of each link on a three-part scale from "Low" to "High."

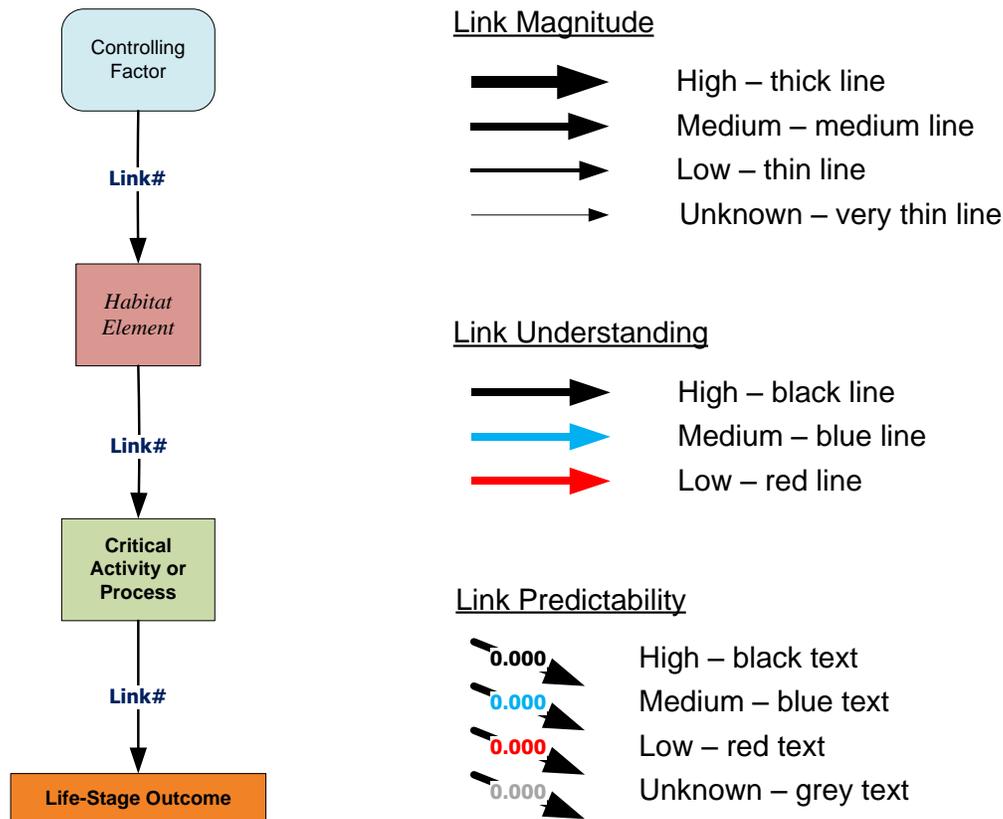
Constructing the CEM for each life stage involves identifying, assembling, and rating each causal link one at a time. Analyses of the resulting information for each life stage can then identify the causal relationships that most strongly support or limit life-stage outcomes, support or limit the rate of each critical biological activity and process, and support or limit the quality of each habitat element, as

**MacNeill’s Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

that element affects other habitat elements or affects critical biological activities and processes. Analyses also can identify which, among these potentially high-impact relationships, are not well understood.

All potential causal links – among controlling factors, habitat elements, critical biological activities and processes, and life-stage outcomes – affecting each life stage are recorded in a spreadsheet. This spreadsheet is then used to record information on the character and direction, magnitude, predictability, and scientific understanding for each causal link, along with the underlying rationale and citations, for each life stage.

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



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

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

The discussions of quailbush ecology and the individual MNSW life stages in this chapter and the discussion of all four life stages considered together in chapter 7 include analyses of the information contained in the spreadsheet. The analyses highlight causal chains that strongly affect quailbush conditions and the outcomes for each life stage, and they identify important causal relationships with high scientific uncertainty.

## **QUAILBUSH ECOLOGY**

The quailbush is the host plant for the entire MNSW life cycle. The CEMs for all four MNSW life stages identify (a) quailbush patch size and structure and (b) quailbush shrub condition as important habitat elements. The CEMs for the pupal, larval, and adult life stages identify quailbush litter condition as an important habitat element. Additionally, the CEM for the adult life stage identifies quailbush patch distribution as another important habitat element. The CEMs for the four life stages show that the factors affecting these four habitat elements – the effects of the six controlling factors, the interactions of the four habitat elements with each other, and their interactions with other habitat elements – are the *same for all four MNSW life stages*. This section of chapter 6 summarizes this shared suite of causal relationships. Chapter 7 also discusses causal relationships across all four life stages. The discussion of quailbush ecology is presented here rather than later in chapter 7 because it provides a foundation for understanding the CEMs for all four MNSW life stages.

Figure 3 shows the causal relationships that directly or indirectly shape quailbush litter condition, quailbush patch distribution, quailbush patch size and structure, and quailbush shrub condition along the LCR valley. It also summarizes information reviewed to prepare the CEMs for all four MNSW life stages and shows that only quailbush shrub condition has any large effect on quailbush litter condition. However, the CEM rates this effect as having only medium magnitude because other factors, such as fire, also affect litter condition. No controlling factors directly affect quailbush litter condition. However, onsite water management and onsite fire management likely affect quailbush litter condition closely, but indirectly, through their effects on the fire and inundation regimes at MNSW habitat sites. As with the many causal links shown on figure 3, the effect of quailbush shrub condition on quailbush litter condition has not been a specific subject of investigation and therefore is not well understood.

Quailbush patch distribution is shaped by only a single but well-understood factor, offsite land management and use. Many other factors affecting soils and disturbance patterns would have shaped the distribution of quailbush patches across the LCR valley under natural conditions; however, none of these other factors matter under present conditions.

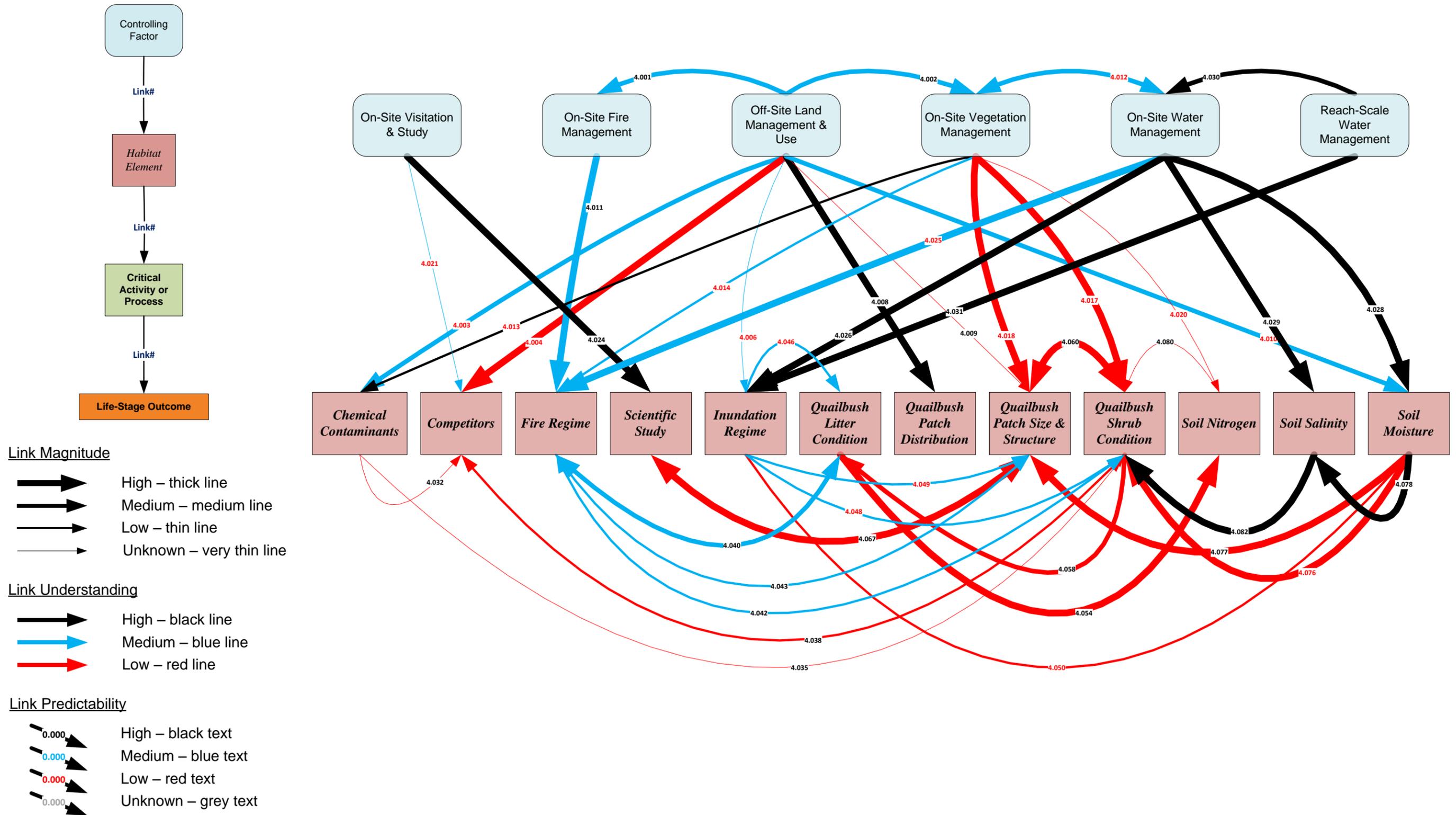


Figure 3.—Causal relationships affecting quailbush ecology across all MNSW life stages.

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Quailbush patch size and structure is affected directly by one controlling factor and several other habitat elements, which in turn are shaped by other controlling factors. Onsite vegetation management, a controlling factor, strongly affects quailbush patch size and structure. However, MNSW habitat sites are embedded within larger habitat conservation sites. The literature reviewed for this CEM does not discuss how site-scale vegetation management affects or takes into account the management of quailbush patches. The literature also indicates that quailbush patches sometimes may be managed to facilitate scientific study, such as through the clearing of transects. However, the literature does not document how this activity may have affected habitat structure in ways that might in turn affect MNSW behavior. Quailbush patch size and structure also depend on quailbush shrub condition. Other quailbush shrubs at a site are the most likely sources for seeding new shrubs, and patch vertical and horizontal structure depends on the condition of the individual shrubs that comprise a patch. However, this interplay has not specifically been studied. Quailbush patch size and structure also depend on the sizes of the areas available with suitable conditions of soil moisture. However, the literature does not provide much information on this interplay between soil moisture and patch size.

Disturbances from fire and inundation can strongly shape quailbush patch size and structure. However, both disturbance processes are highly managed at any MNSW habitat sites for which the LCR MSCP is responsible. The literature therefore documents only limited impacts of fire and inundation on quailbush patch size and structure. Controlling factors that shape the fire and inundation regimes on MNSW habitat sites include onsite fire management, onsite vegetation management, onsite water management, and reach-scale water management. Quailbush patches conceivably may also be artificially truncated at their borders by surrounding land management activities. However, the literature reviewed for this CEM provides no information on this potential interaction, so its magnitude is rated as "Unknown."

Quailbush shrub condition also is affected directly by one controlling factor and several other habitat elements, which in turn are again shaped by other controlling factors. Onsite vegetation management, a controlling factor, strongly affects quailbush shrub condition. However, as noted above concerning quailbush patch size and structure, MNSW habitat sites are embedded within larger habitat conservation sites. The literature reviewed for this CEM does not discuss how site-scale vegetation management affects or takes into account the management of quailbush patches or individual shrubs. Quailbush shrub condition also depends on quailbush patch size and structure. Other quailbush shrubs at a site may both shelter and compete for soil moisture and space with other quailbush shrubs; however, this interplay has not specifically been studied.

Quailbush shrub condition also depends on both soil moisture and soil salinity. Quailbush shrubs tolerate a relative wide range of conditions of soil moisture and soil salinity. However, they achieve their greatest size and lushness only within a

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

narrower range of moisture and salinity, within which they compete effectively against other plants (Meyer 2005). The effects of soil salinity on quailbush shrub condition are relatively better documented (Meyer 2005) as are the effects of soil moisture variation on soil salinity in desert soils. Both soil moisture and soil salinity, in turn, are strongly affected by onsite water management practices at MNSW habitat sites. The effects of water management practices on soil salinity are widely studied in irrigated desert regions, and irrigation water salinity and its effects are a topic of concern throughout the LCR valley. Offsite land management practices may also affect soil moisture at MNSW habitat sites to the extent that such practices affect water table elevations at MNSW habitat sites.

The literature contains suggestions that adding nitrogen to soils at quailbush patches might improve quailbush shrub condition, specifically leaf-nitrogen content (see chapter 4, "Soil Nitrogen"). However, quailbush roots support microbial communities that fix nitrogen. Adding nitrogen to soils in quailbush patches therefore may have little effect on soil nitrogen availability for the shrubs. The literature does not record any experiments to evaluate this potential interaction. Theoretically, too, decomposition of their own leaf litter may carry reactive nitrogen back into the soil beneath quailbush shrubs. However, this process has not specifically been studied. The CEM also considers the possibility of chemical contamination as a factor that could affect quailbush shrub condition. However, the literature reviewed and the experts consulted for this CEM reported no known instances of actual contamination.

Disturbances from fire and inundation are capable of strongly shaping quailbush shrub condition. However, both disturbance processes are highly managed at any MNSW habitat sites for which the LCR MSCP is responsible, and the literature documents only limited impacts of fire and inundation on quailbush shrub condition (see chapter 4). As noted above, the controlling factors that shape the fire and inundation regimes on MNSW habitat sites include onsite fire management, onsite vegetation management, onsite water management, and reach-scale water management. Plant species that compete with quailbush for habitat, and insects that feed on quailbush shrubs, and therefore may compete with MNSW larvae, presumably also may affect quailbush condition. However, the literature reviewed for this CEM presents no evidence of the latter types of interactions, and the relationships have not specifically been studied. On the other hand, to the extent that such relationships exist, offsite land management practices may significantly affect the available pool of potential competitors.

## **MNSW LIFE STAGE 1 – EGG STAGE**

As described in chapter 2, this life stage includes the eggs from all broods in a year (see discussion of broods under "MNSW Life Stage 4 – Adult Stage," below). The life stage has a single life-stage outcome, designated  $S_E$  on figure 1, survivorship over the course of the life stage.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Figure 4 shows the causal relationships that affect MNSW egg survivorship along the LCR valley represented in the CEM for this life stage. As the CEM does for all other MNSW life stages, the CEM for the egg stage includes quailbush patch size and structure and quailbush shrub condition as important habitat elements. Figure 3, above, already summarizes the causal relationships that affect these two aspects of quailbush ecology (see “Quailbush Ecology,” above). Figure 5 provides a simplified version of figure 4, excluding any relationships that affect only quailbush ecology.

Figure 5 shows that two (of seven) critical biological activities and processes affect egg survivorship, both with high magnitude: physiological stress and predation. Based on general ecological principles and studies of butterflies in general, infection, chemical contamination, or exposure to extremes of heat or wind could lower egg survivorship through physiological stress, with thermal stress the most likely suspect for MNSW eggs. Similarly, based on general ecological principles and studies of butterflies in general, predation may be readily presumed to lower egg survivorship by directly removing individuals from the population. However, none of the information reviewed for this CEM addresses either the causes or rates of egg mortality. The two causal relationships that directly affect egg survivorship therefore are hypothetical, with low understanding.

Only one habitat element is hypothesized to affect the rate of predation with any significant magnitude: predators, defined as the composition, spatial and temporal distributions, abundances, and activity levels of invertebrates and vertebrates that prey on MNSW eggs. The magnitude of this relationship is hypothesized to be high, but none of the information reviewed for this CEM identifies any particular species as potential predators on MNSW eggs, resulting in a rating of low for understanding (see chapter 4, “Predators”).

Two habitat elements are hypothesized to affect the intensity of physiological stress experienced by MNSW eggs with any significant magnitude: quailbush shrub condition and quailbush patch size and structure. Both habitat elements affect the amount of shade provided to MNSW eggs by the surrounding vegetation, beginning with the shade provided by the individual shrub on which the eggs lie and extending to the shade provided by the patch as a whole, including larger woody vegetation within and surrounding the patch. The magnitudes of these effects are hypothesized to be high based on the importance of shading for temperature extremes for later MNSW life stages. However, none of the information reviewed for this CEM directly discusses these potential effects, resulting in a rating of low for understanding (see chapter 4, “Quailbush Shrub Condition” and “Quailbush Patch Size and Structure”).

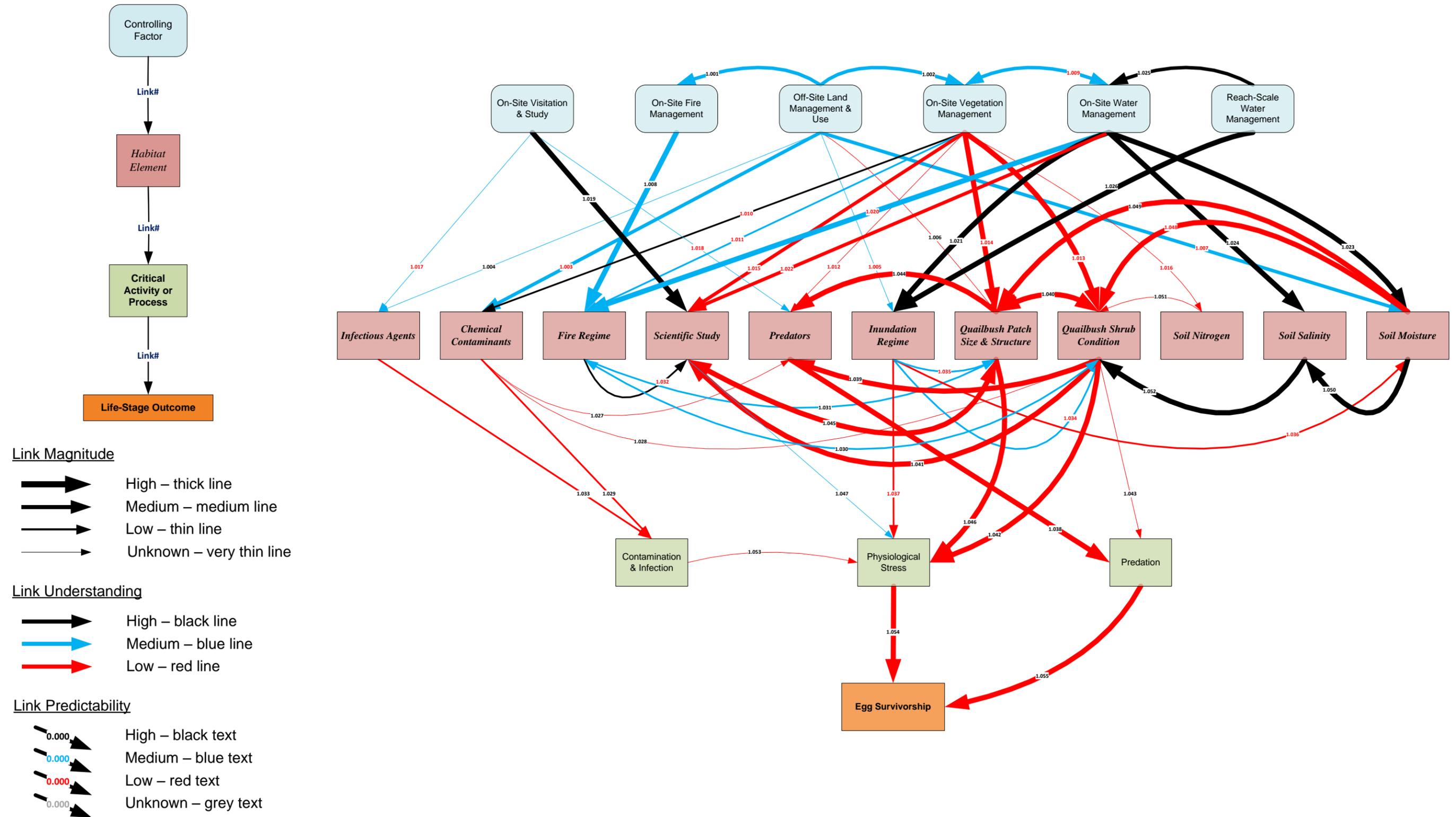


Figure 4.—MNSW Life Stage 1 – Egg Stage, complete model.

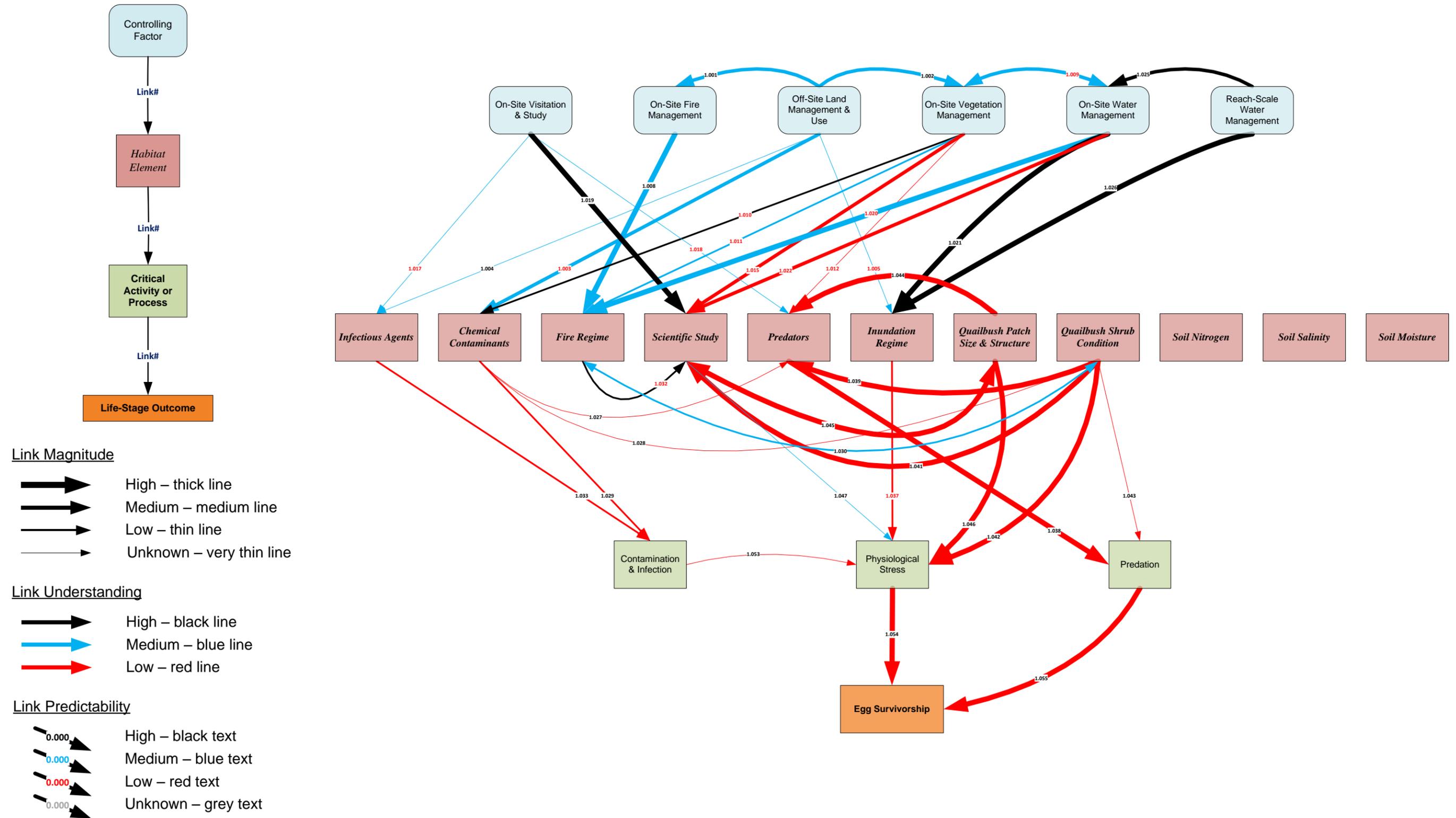


Figure 5.—MNSW Life Stage 1 – Egg Stage, omitting links that affect only quailbush ecology.

## MNSW LIFE STAGE 2 – LARVAL STAGE

As described in chapter 2, this life stage includes all instars for all larvae (caterpillars) produced by all broods in a year (see discussion of broods under “MNSW Life Stage 4 – Adult Stage,” below). The life stage has a single life-stage outcome, designated  $S_L$  on figure 1, survivorship over the course of the life stage.

Figure 6 shows the causal relationships that affect MNSW larval survivorship along the LCR valley represented in the CEM for this life stage. As the CEM does for all other MNSW life stages, the CEM for the larval stage includes quailbush patch size and structure and quailbush shrub condition as important habitat elements. Figure 3, above, already summarizes the causal relationships that affect these two aspects of quailbush ecology (see “Quailbush Ecology,” above). Figure 7 provides a simplified version of figure 6, excluding any relationships that affect only quailbush ecology.

Figure 7 shows that three (of seven) critical biological activities and processes affect larval survivorship, all with high magnitude: feeding/watering, physiological stress, and predation. MNSW larvae obtain all their water through their feeding on quailbush leaves. Other things being equal, greater success in feeding should result in a higher rate of larval survivorship. The CEM also hypothesizes that, in theory, higher survivorship could also result in greater competition for food resources among MNSW larvae, which in turn could dampen survivorship. However, none of the literature reviewed or experts consulted for this CEM report any evidence of competition for food (crowding) among MNSW larvae let alone sufficient crowding to reduce feeding success. The relationship between feeding success and survivorship among MNSW larvae is rated medium for understanding because, although well understood for butterflies in general, the relationship has not been studied systematically for MNSW of any life stage.

Based on general ecological principles and studies of butterflies in general, infection, chemical contamination, or exposure to extremes of heat or wind could lower larval survivorship through physiological stress, with thermal stress the most likely suspect for MNSW larvae. Similarly, based on general ecological principles and studies of butterflies in general, predation may be readily presumed to lower larval survivorship by directly removing individuals from the population. However, none of the information reviewed for this CEM addresses either the causes or rates of larval mortality. The three causal relationships that directly affect larval survivorship therefore are hypothetical, with low understanding.

The three critical biological activities and processes that affect MNSW larval survivorship, in turn, are affected strongly by other critical biological activities and processes. In general, successful feeding and watering are crucial to

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

minimizing physiological stress in butterflies in all life stages. However, this relationship has not been studied specifically among MNSW larvae except through studies of the nutritional quality of quailbush shrubs. The hypothesized relationship therefore is rated high for magnitude but low for understanding.

In turn, MNSW larval hiding/resting behaviors are hypothesized to reduce both larval physiological stress and mortality due to predation. MNSW larvae spend all of their time within the quailbush canopy and mostly within their leaf shelters. The general literature on such shelters suggests that they provide protection from extremes of air temperature, humidity, and wind, and from intense precipitation as well as from predators. However, most information on how MNSW actually use shelter to cope with air temperature extremes only concerns MNSW adults, which use the quailbush canopy rather than individual leaf shelters for protection. The literature reviewed for this CEM provides no information on whether or how MNSW larvae actually may be affected (stressed) by temperature extremes or other potential environmental sources of physiological stress or how they use their leaf shelters or position themselves within the canopy to cope with temperature variation.

Indeed, little is known about MNSW larval movements within the quailbush canopy in general. Similarly, the literature reviewed for this CEM provides no information on potential predators on MNSW of any life stage (see chapter 3, "Predation," and chapter 4, "Predators") nor on ways in which MNSW hiding behaviors may affect rates of predation. Wiesenborn (2010) identifies this lack of information on predation (and parasitism) as a significant gap in knowledge of the species. The ratings for link magnitude for the effects of MNSW larval hiding/resting behavior on larval physiological stress or mortality due to predation therefore are based on the adult ratings.

Only one habitat element is hypothesized to affect the rate of predation on MNSW larvae with any significant magnitude: predators, defined as the composition, spatial and temporal distributions, abundances, and activity levels of invertebrates and vertebrates that prey on MNSW larvae. The magnitude of this relationship is hypothesized to be high, but none of the information reviewed for this CEM identifies any particular species as potential predators on MNSW larvae, resulting in a rating of low for understanding (see chapter 4, "Predators"). As noted above, Wiesenborn (2010) identifies this lack of information on predation (and parasitism) as a significant gap in knowledge of the species.

Two habitat elements are hypothesized to affect the intensity of physiological stress experienced by MNSW larvae with any significant magnitude: quailbush shrub condition and quailbush patch size and structure. Both habitat elements affect the amount of shade provided to MNSW larvae by the surrounding vegetation, beginning with the shade provided by the individual shrub on which the larvae live and extending to the shade provided by the patch as a whole,

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

including larger woody vegetation within and surrounding the patch. The magnitudes of these effects are hypothesized to be high based on the importance of shading for temperature extremes for later MNSW life stages. However, none of the information reviewed for this CEM directly discusses these potential effects, resulting in a rating of low for understanding (see chapter 4, “Quailbush Shrub Condition” and “Quailbush Patch Size and Structure”).

Quailbush shrub condition strongly affects MNSW larval feeding/watering success. This is one of the best-studied aspects of MNSW ecology. As discussed above, quailbush leaf-water content and leaf-nitrogen content, along with overall canopy lushness (low incidence of dry leaves), affect larval feeding and acquisition of water, with a leaf-water content > 64 percent and a leaf-nitrogen content > 3.2 percent providing optimal water and nutritional quality (see chapter 2, “Larval Stage”; chapter 3, “Feeding/Watering”; and chapter 4, “Quailbush Shrub Condition”). Larval “selection” among plants and leaves for feeding and watering is actually an outcome of selection by ovipositing females (see “MNSW Life Stage 4 – Adult Stage,” below). Conversely, MNSW larval feeding/watering behaviors affect the scientific study of MNSW by affecting larval visibility within the quailbush shrub canopy.

Finally, two habitat elements affect MNSW larval hiding/resting behavior. MNSW larvae are hypothesized to descend into the quailbush leaf litter beneath their natal shrub to overwinter and pupate (see chapters 2 and 3). The thickness, dryness/moisture, and stability of the leaf litter therefore presumably affect the suitability of the litter as hiding and resting habitat for both these life stages. In turn, quailbush shrub condition potentially affects larval hiding/resting behavior by affecting the suitability of leaves for forming shelters. However, the literature does not indicate in what ways leaf condition might affect leaf suitability for forming shelters. On the other hand, quailbush condition does affect the density of shade at different elevations within individual shrubs, and the availability of shade potentially could affect the time of day and duration of larval emergence from their shelters to feed (Wiesenborn 1999; Pratt and Wiesenborn 2009; Nelson et al. 2014, 2015). The shade of the canopy appears to help MNSW adults tolerate high air temperatures (Wiesenborn 1999, 2010), to which they may be less physiologically adapted than some other butterfly species (Wiesenborn 1999). The CEM applies this same reasoning to the MNSW larval life stage. However, none of the literature reviewed for this CEM provides specific information on how quailbush leaf litter or quailbush shrub condition actually affect MNSW larval hiding/resting behaviors. Consequently, these links are both rated as low for understanding. Conversely, MNSW larval hiding/resting behaviors affect the scientific study of MNSW by affecting larval visibility within the quailbush shrub canopy.

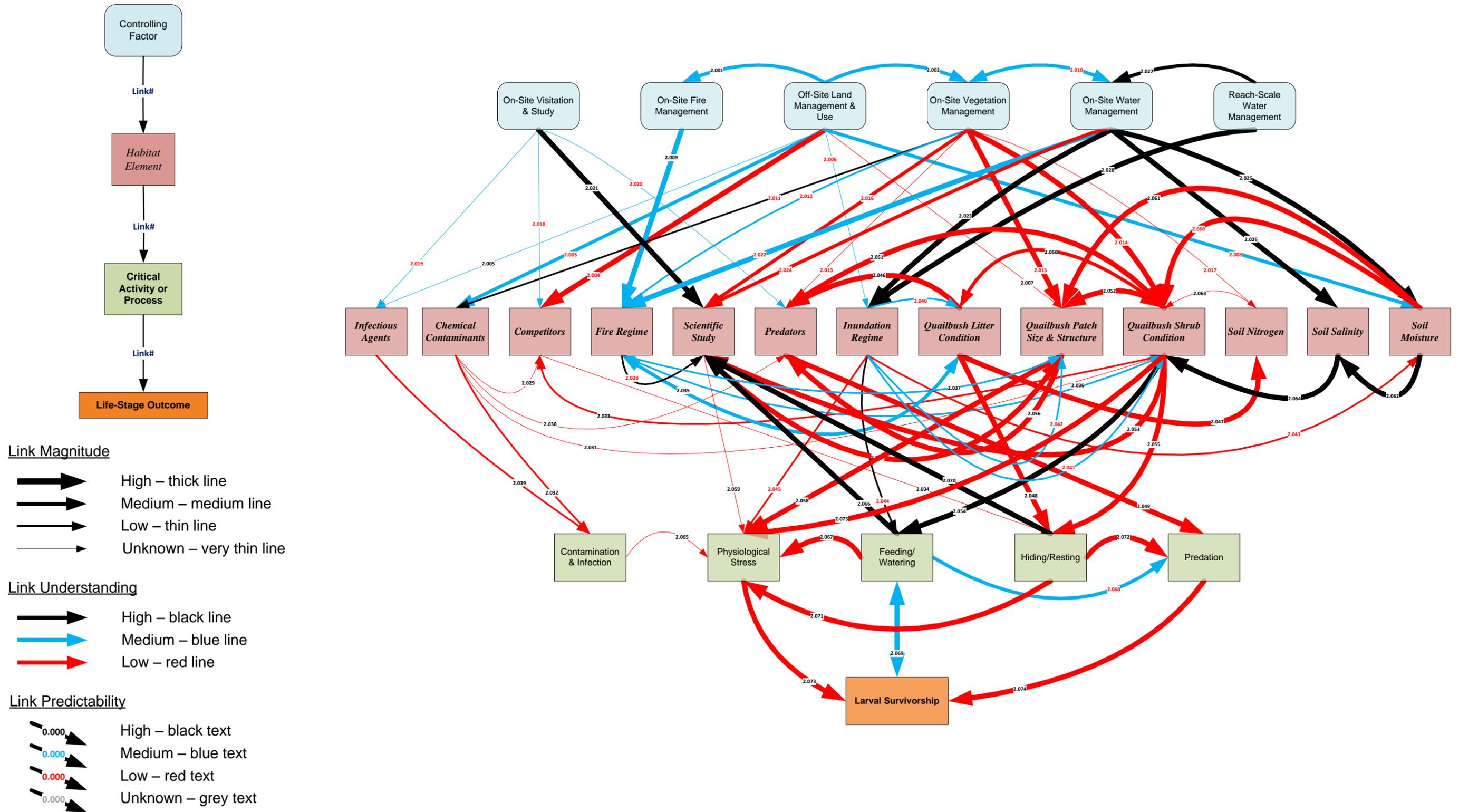


Figure 6.—MNSW Life Stage 2 – Larval Stage, complete model.

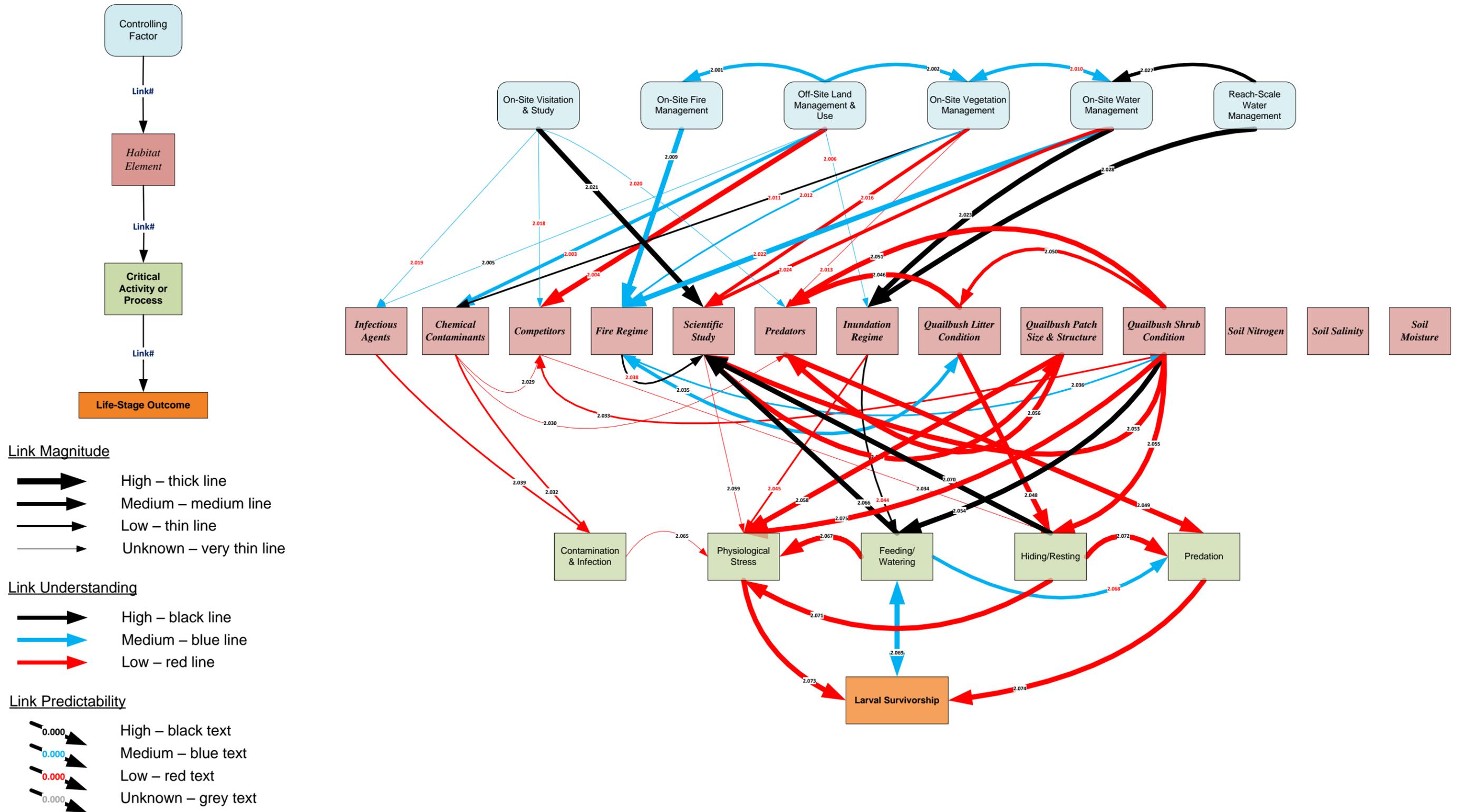


Figure 7.—MNSW Life Stage 2 – Larval Stage, omitting links that affect only quailbush ecology.

## MNSW LIFE STAGE 3 – PUPAL STAGE

As described in chapter 2, this life stage includes all pupae from all broods in a year (see discussion of broods under “MNSW Life Stage 4 – Adult Stage,” below). The life stage has a single life-stage outcome, designated  $S_P$  on figure 1, survivorship over the course of the life stage.

Figure 8 shows the causal relationships that affect MNSW pupal survivorship along the LCR valley represented in the CEM for this life stage. As the CEM does for all other MNSW life stages, the CEM for the pupal stage includes quailbush patch size and structure and quailbush shrub condition as important habitat elements. Figure 3, above, already summarizes the causal relationships that affect these two aspects of quailbush ecology (see “Quailbush Ecology,” above). Figure 9 provides a simplified version of figure 8, excluding any relationships that affect only quailbush ecology.

Figure 9 shows that two (of seven) critical biological activities and processes affect pupal survivorship, both with high magnitude: physiological stress and predation. Based on general ecological principles and studies of butterflies in general, infection, chemical contamination, inundation of the leaf litter in which MNSW pupate, or exposure to extremes of heat or wind could lower pupal survivorship through physiological stress. Similarly, based on general ecological principles and studies of butterflies in general, predation may be readily presumed to lower pupal survivorship by directly removing individuals from the population. However, none of the information reviewed for this CEM addresses either the causes or rates of pupal mortality. The two causal relationships that directly affect pupal survivorship therefore are hypothetical, with low understanding.

The two critical biological activities and processes that affect MNSW larval survivorship, in turn, are affected strongly by another critical biological activity. MNSW larval selection of hiding/resting locations in which to pupate is hypothesized to affect pupal physiological stress and mortality due to predation. Pupae in locations subject to extremes of heat or to inundation are more likely to experience physiological stress, and pupae in locations easily accessible to predators are more likely to be consumed by those predators, other things being equal. However, the literature reviewed for this CEM provides no information on whether MNSW larvae select locations for pupation in ways that reduce exposure to environmental stressors or to predators, whether exposure to environmental stressors affects pupal health, or how predation affects pupal mortality. As noted earlier, Wiesenborn (2010) identifies the lack of information on predation (and parasitism) as a significant gap in knowledge of MNSW ecology. The relationship between hiding/resting location and physiological stress is assigned a medium rating for understanding based on the sensitivity of MNSW adults to temperature extremes (see “MNSW Life Stage 4 – Adult Stage,” below).

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Only one habitat element is hypothesized to affect the rate of predation on MNSW pupae with any significant magnitude: predators, defined as the composition, spatial and temporal distributions, abundances, and activity levels of the invertebrates and vertebrates that prey on MNSW pupae. The magnitude of this relationship is hypothesized to be high, but none of the information reviewed for this CEM identifies any particular species as potential predators on MNSW pupae, resulting in a rating of low for understanding (see chapter 4, “Predators”). Again, as noted above, Wiesenborn (2010) identifies the lack of information on predation (and parasitism) as a significant gap in knowledge of MNSW ecology.

Two habitat elements are hypothesized to affect the intensity of physiological stress experienced by MNSW pupae with any significant magnitude: quailbush shrub condition and quailbush patch size and structure. Both habitat elements affect the amount of shade provided to MNSW pupae within the leaf litter by the surrounding vegetation, beginning with the shade provided by the individual shrub beneath which the pupae is located and extending to the shade provided by the patch as a whole, including larger woody vegetation within and surrounding the patch. The magnitudes of these effects are hypothesized to be high based on the importance of shading for temperature extremes for MNSW adults. However, none of the information reviewed for this CEM directly discusses these potential effects on MNSW pupae, resulting in a rating of low for understanding (see chapter 4, “Quailbush Shrub Condition” and “Quailbush Patch Size and Structure”).

The model also identifies inundation as a potential cause of physiological stress for MNSW pupae but assigns this relationship a low magnitude. Inundation occurs only rarely in MNSW habitat sites, with limited duration, and subsequent weather conditions can quickly dry MNSW sites again. Consequently, harmful inundation events (i.e., events of sufficient duration and depth to harm MNSW pupae either in the leaf litter or on lower branches) are likely rare. However, the effects of inundation on MNSW pupae have not been studied.

One habitat element affects MNSW pupal hiding/resting location quality. As noted earlier (see “MNSW Life Stage 2 – Larval Stage,” above), MNSW larvae reportedly descend into the quailbush leaf litter beneath their natal shrub to overwinter and pupate (see chapters 2 and 3). The thickness, dryness/moisture, and stability of the leaf litter therefore presumably affect the suitability of the litter as hiding/resting habitat for the pupae. However, none of the literature reviewed for this CEM provides specific information on how quailbush leaf litter condition actually affects MNSW pupal hiding/resting habitat quality. Consequently, this link is rated as low for understanding. Conversely, MNSW pupal hiding/resting location condition presumably affects the scientific study of MNSW by affecting pupal visibility within the leaf litter.

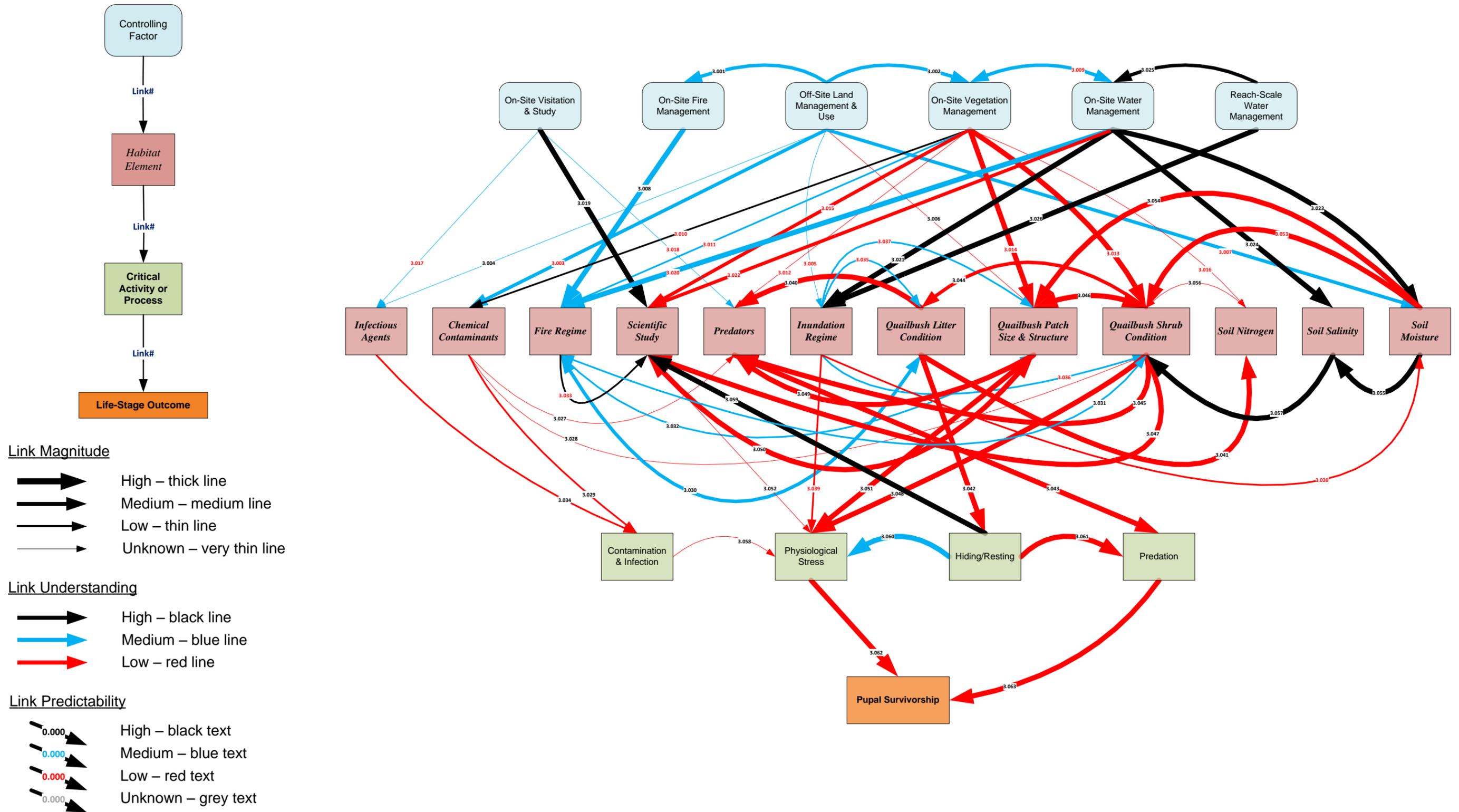


Figure 8.—MNSW Life Stage 3 – Pupal Stage, complete model.

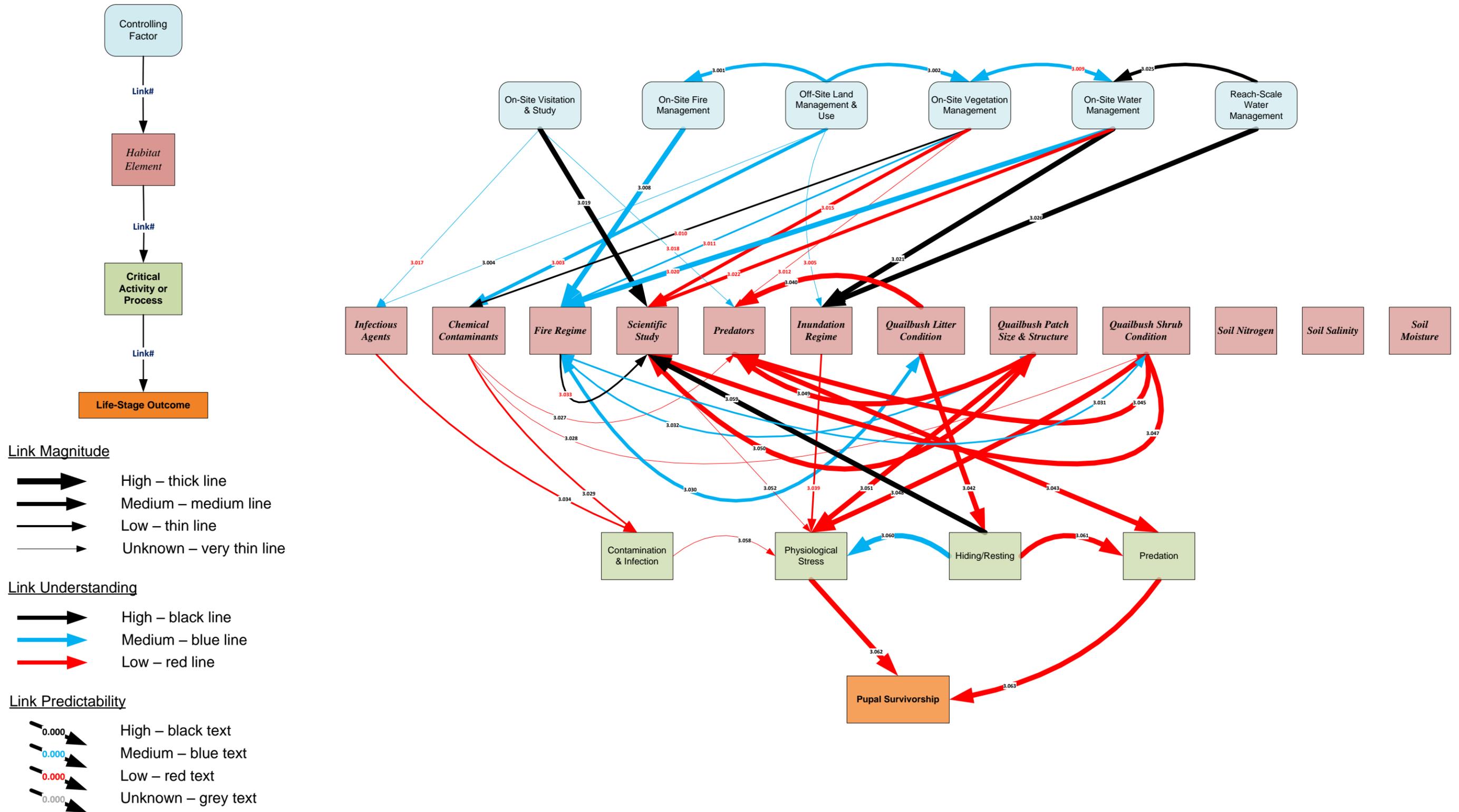


Figure 9.—MNSW Life Stage 3 – Pupal Stage, omitting links that affect only quailbush ecology.

## NECTAR SOURCE ECOLOGY

This section of chapter 6 summarizes the causal relationships that affect the plants on which MNSW adults forage for nectar. MNSW adult ecological dynamics depend on the ecological dynamics of quailbush and nectar sources. Figure 10 shows the causal relationships that directly or indirectly shape the species, visibilities, size ranges, spatial and temporal distributions, abundances, and nectar volumes and nutritional quality of plants that MNSW adults use as nectar sources.

The habitat element, “nectar sources,” on figure 10 represents the species, visibilities, size ranges, spatial and temporal distributions, abundances, and nectar volumes and nutritional quality of MNSW nectar sources (see chapter 4, “Nectar Sources”). A comparison of figures 3 and 10 shows that MNSW nectar sources are affected by the same suite of causal relationships that affect quailbush ecology, although with different magnitudes.

MNSW nectar sources may occur within occupied quailbush patches or across the landscape surrounding these patches. As noted earlier (see chapter 3, “Feeding/Watering”), the literature reviewed for this CEM provides little data on foraging distances. Wiesenborn (1997) observed individuals flying across distances of approximately 4 m between quailbush shrubs and mesquite (potentially to feed on extrafloral nectar) and also observed MNSW traveling approximately 0.25 kilometer to stands of sweetbush when no other closer nectar sources were available. The CEM hypothesizes that the visibilities, size ranges, spatial and temporal distributions, abundances, and nectar volumes and nutritional quality of MNSW nectar sources within the foraging radii of MNSW adults are affected with high magnitude by the distributions of soil nitrogen and soil moisture, fire history, and offsite land management and use.

Specifically, soil nitrogen levels are hypothesized to affect both the distribution of nectar sources and the nutritional quality of their nectar. Soil nitrogen conditions presumably affect the availability, quality, and spatial distribution of nectar sources, although the literature reviewed for this CEM does not systematically address this topic. Marler et al. (2001) found that saltcedar produces more stems and achieves higher shoot biomass, total biomass, and shoot:root biomass ratio values with increasing soil nitrogen availability, in applications of mixed N- and P-fertilizers. In contrast, the review of saltcedar ecology by Zouhar (2003) makes no mention of the sensitivity of saltcedar to soil nitrogen levels. Honey mesquite fixes nitrogen (Bailey 1976) and, as with quailbush, its condition therefore may not be sensitive to soil nitrogen levels. The literature reviewed for this CEM otherwise did not address the effects of soil nitrogen levels on MNSW nectar source availability. On the other hand, Pratt and Wiesenborn (2009), Wiesenborn (2010), Wiesenborn and Pratt (2010), and Nelson et al. (2015) suggest that MNSW adults prefer nectar with higher concentrations of amino acids. If nectar

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

sources vary in amino acid production in their nectar, it is possible that variations in soil nitrogen levels contribute to variations in nectar amino acid concentrations.

Soil moisture conditions presumably affect the availability, quality, and spatial distribution of nectar sources. For example, heliotrope can dry up entirely under very dry conditions (Wiesenborn 2012). In contrast, alfalfa can produce more blooms with more nectar immediately following significant rainfall and thereby attract MNSW even across moderate distances (Reclamation 2013). However, the literature reviewed for this CEM does not systematically address the ways in which soil moisture may affect nectar source density, spatial distributions, or the masses or quality of the nectar they produce.

Fire can greatly diminish or destroy patches of nectar sources, including trees, but fire disturbance may also open habitat for colonization or re-establishment of flowering plants that MNSW uses as nectar sources. Fire resistance and/or adaptations also vary among MNSW nectar sources. Saltcedar is highly fire adapted: the high moisture content of its leaves make them poorly flammable, and plants can regenerate from root crowns even following top-kill from fire (Zouhar 2003; Nagler et al. 2011). However, its leaf and branch litter are highly flammable and, in dense thickets, may result in a greater frequency of fires and fires of high severity, which destroy even some root crowns (Zouhar 2003). Mesquite, on the other hand, is not fire resistant (Ohmart et al. 1988; Nagler et al. 2011). Among the other nectar sources, only arrowweed, a shrub, resembles saltcedar in being both halophytic and fire resistant (Zouhar 2003). Sweetbush, another shrub, appears to be able to recover from roots and/or seeds following fire (Brown and Minnich 1986). Salt heliotrope, western purslane, alkali mallow, and common purslane are all native perennial herbs adapted to the natural fire regimes of the plant communities in which quailbush occurs (Meyer 2005). They are readily destroyed by fire but able to recolonize burned sites rapidly through seed dispersal from surrounding areas.

Some farm crops, such as alfalfa, are nectar sources for MNSW, and disturbed areas around field margins may also provide habitat for native nectar sources. In turn, use or management of offsite lands for activities other than farming will affect the abundance and distribution of nectar sources, including mesquite and saltcedar. For example, activities that either favor or disfavor saltcedar or mesquite colonization or suppression will affect the distribution of these potential floral and extrafloral nectar sources.

Additionally, onsite vegetation management at MNSW habitat sites is hypothesized to affect the visibilities, size ranges, spatial and temporal distributions, abundances, and nectar volumes and nutritional quality of MNSW nectar sources within these sites, with medium magnitude. Specifically, site management actions such as intentional soil disturbance, removal of unwanted vegetation, and, potentially, application of fertilizers, can affect the conditions that shape the presence and abundance of nectar sources on MNSW habitat sites.



## MNSW LIFE STAGE 4 – ADULT STAGE

As described in chapter 2, this life stage includes all individuals that emerge as adults in a year, beginning with those that emerge from the pupae from the last brood of the previous year. This life stage has three life-stage outcomes: (1) the rate of survivorship of adults long enough following emergence to mate, designated  $S_A$  on figure 1; (2) the rate of production of viable eggs per surviving adult in a year, designated  $R_A$  on figure 1; and (3) the rate of successful dispersal of adults to other habitat patches, designated  $D_A$  on figure 1.

Figure 11 shows the causal relationships that affect MNSW adult life-stage outcomes along the LCR valley represented in the CEM for this life stage. As the CEM does for other MNSW life stages, the CEM for the adult life stage includes quailbush patch size and structure, quailbush shrub condition, and quailbush litter condition as important habitat elements. Additionally, the CEM for the adult life stage includes two habitat elements not applicable to any other life stage: nectar sources and quailbush patch distribution. Figure 3, above, already summarizes the causal relationships that affect quailbush ecology, including quailbush patch distribution (see “Quailbush Ecology,” above). In turn, figure 10, above, already summarizes the causal relationships that affect nectar source ecology (see “Nectar Source Ecology,” above). Figure 12 provides a simplified version of figure 11, excluding any relationships that affect only quailbush or nectar source ecology.

Figure 12 shows that three (of seven) critical biological activities and processes affect adult survivorship, all with high magnitude: feeding/watering, physiological stress, and predation. MNSW adults obtain all their water through their feeding on nectar leaves. Other things being equal, greater success in feeding should result in a higher rate of adult survivorship (i.e., in greater adult longevity). The CEM also hypothesizes that, in theory, greater longevity could also result in greater competition for food resources among MNSW adults, which in turn could dampen longevity in feedback. However, none of the literature reviewed or experts consulted for this CEM report any evidence of competition for food (crowding) among MNSW adults let alone evidence of sufficient crowding to reduce feeding success. The relationship between feeding success and survivorship among MNSW adults is rated medium for understanding because, although well understood for butterflies in general, the relationship has not been studied systematically for MNSW of any life stage.

Based on general ecological principles and studies of butterflies in general, infection, chemical contamination, or exposure to extremes of heat or wind could lower adult survivorship through physiological stress, with thermal stress the most likely suspect for MNSW adults. MNSW may be less physiologically adapted to high air temperatures than are some other butterfly species (Wiesenborn 1999)

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

and appear to seek the shade of quailbush canopies to help avoid such temperatures (Wiesenborn 1999, 2010a) (see chapter 3, "Hiding/Resting"). MNSW adults may also preferentially occupy quailbush located near trees, the shade of which may provide some additional protection against the heat (Wiesenborn 1997; Pratt and Weisenborn 2011; Nelson et al. 2014).

Similarly, based on general ecological principles and studies of butterflies in general, predation may be readily presumed to lower adult survivorship by directly removing individuals from the population. However, the literature reviewed for this CEM provides no information on potential predators on MNSW of any life stage (see chapter 3, "Predation"). As noted throughout this CEM, Wiesenborn (2010a) identifies the lack of information on predation (and parasitism) as a significant gap in knowledge of MNSW ecology.

Figure 12 shows that no critical biological activities and processes strongly directly affect the MNSW adult dispersal rate. Instead, this rate depends most strongly on a single habitat element, quailbush patch distribution, and the sizes, numbers, and proximity of quailbush patches to each other across the landscape (see chapter 4, "Quailbush Patch Distribution"). As discussed earlier (see chapter 2), the proximity of quailbush patches to each other should affect the likelihood that MNSW adults can fly from one patch to another. However, as also discussed earlier (see chapter 2 and also chapter 4, "Quailbush Patch Distribution"), the process of MNSW dispersal is little understood.

Figure 12 shows that two critical biological activities and processes strongly directly affect the MNSW adult reproductive output rate: predation and ovipositing. The rate at which MNSW adult females of a particular brood successfully oviposit viable eggs necessarily significantly affects the reproductive output rate of the brood (together with female survivorship and mating success rates). However, the literature reviewed for this CEM does not address the topic, so a great deal remains unknown. In turn, predation lowers the reproductive output rate by removing adults from the pool of females that mate and, subsequently, oviposit. However, the literature reviewed for this CEM also does not address the topic, so again, much remains unknown.

The critical biological activities and processes that affect MNSW adult survivorship, dispersal, and reproduction, in turn, are affected strongly by other critical biological activities and processes. In general, successful feeding and watering are crucial to minimizing physiological stress in butterflies in all life stages. However, this relationship has not been studied specifically among MNSW adults. The hypothesized relationship therefore is rated high for magnitude but low for understanding.

Greater success in feeding presumably also should result in greater success in ovipositing. As noted in chapter 4, "Nectar Sources," and in the discussion of the

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

link between feeding/watering and physiological stress, MNSW females ingest significant quantities of nectar, preferentially select flowers with higher nectar sugar content, and spend more time feeding when flowers have lower sugar content (Wiesenborn 2010, 2011; Wiesenborn and Pratt 2010). In contrast, MNSW males do not ingest significant quantities of nectar, do not select flowers with higher nectar sugar content, and do not spend either more or less time feeding when flowers have lower sugar content (Wiesenborn 2010, 2011; Wiesenborn and Pratt 2010). Further, MNSW appear to identify potential floral nectar sources based on the visible color reflectance of flowers observed during flight but appear to land preferentially on flowers based on UV light absorbance (Pratt and Wiesenborn 2009; Reclamation 2009; Wiesenborn 2010). They also prefer flowers in open sun rather than in shade (Wiesenborn and Pratt 2010). They prefer flowers in the yellow-to-purple visible color reflectance range of salt heliotrope flowers, the most common and most frequently selected of native floral nectar sources (Pratt and Wiesenborn 2009; Reclamation 2009; Wiesenborn 2010a, 2010b, 2011). Heliotrope flower centers are yellow when young, turning purple with age (Wiesenborn 2011). The amount of nectar and sugar mass in heliotrope flowers decline as flowers age and turn color from yellow- to purple-centered along a cyme, although purple-centered flowers generally outnumber the yellow-centered ones as a cyme ages (Wiesenborn 2011). Additionally, Wiesenborn and Pratt (2010) found that females selected nectar sources with sugar masses of  $0.30 \pm 0.07$  mg (males:  $0.13 \pm 0.02$  mg). The authors also suggest that MNSW females – like other butterflies described in the literature – may prefer nectar with higher concentrations of amino acids (see also Pratt and Wiesenborn 2009; Wiesenborn 2010; Nelson et al. 2015). Nelson et al. (2015) specifically suggest that females may seek nectar richer in amino acids if their natal quailbush provided them (as larvae) with leaves of lower nutritional quality. All these facts suggest that feeding/watering success must be crucial to ovipositing success since females need such high nutritional inputs for only one purpose: ovipositing.

Mating success and female health (the converse of physiological stress), plus the availability of suitable laying sites (see below), presumably also strongly affect ovipositing success. None of the literature reviewed for this CEM addresses MNSW mating rates or female health and their relationships to ovipositing rates. However, the relationship between mating success and ovipositing success is given a medium rating for understanding since ovipositing cannot take place without mating.

In turn, MNSW adult hiding/resting behaviors are hypothesized to reduce both adult physiological stress and mortality due to predation. As noted above, MNSW adults position themselves within the quailbush canopy to help reduce their exposure to excessively high air temperatures. At least theoretically, too, adult MNSW within quailbush canopy also would be less visible to predators

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

flying overhead, such as insectivorous birds and flying insects. However, as noted frequently in this report, no data appear to be available on what species prey on MNSW in any life stage.

Numerous habitat elements affect the rates of the critical biological activities and processes that strongly affect the three outcomes for the MNSW adult life stage. As discussed above (this chapter; chapter 3, "Feeding/Watering"; and chapter 4, "Nectar Sources"), and as well studied in the literature, the species, visibilities, size ranges, spatial and temporal distributions, abundances, and nectar volumes and nutritional quality of the plants that MNSW adults use as nectar sources strongly affect feeding/watering success. As also discussed above (this chapter; chapter 3, "Hiding/Resting"; and chapter 4, "Quailbush Patch Size and Structure" and "Quailbush Shrub Condition"), both quailbush patch size and structure and quailbush shrub condition strongly affect MNSW adult hiding/resting behavior and physiological stress associated with excessively high air temperatures.

Additionally, quailbush patch size and structure, quailbush shrub condition, and quailbush litter condition strongly affect MNSW mating behavior. MNSW adult males reportedly "patrol" above leaf litter presumably to increase their chances of encountering females as they emerge from their pupation sites in the litter (see chapter 3, "Mating"). The condition of the leaf litter is hypothesized to affect how quickly MNSW adult males are able to detect emerging females. The density of the quailbush canopy and its proximity to the ground therefore also may be hypothesized to affect the rate of success of males patrolling in these settings. Similarly, the spacing of quailbush shrubs within a patch, and the overall size of the patch, will determine how widely MNSW adult males may patrol during their search for mates while avoiding exposure outside the canopies of the quailbush shrubs that comprise the patch. However, none of these topics concerning MNSW mating have been specifically studied.

Finally, both quailbush shrub condition and quailbush patch size and structure affect MNSW ovipositing. The effects of quailbush shrub condition are well studied. Wiesenborn and Pratt (2008) (see also Reclamation 2009) found MNSW eggs consistently only on plants that met three criteria: canopy diameter > 1.6 m; leaf-moisture content > 64 percent; and leaf-nitrogen content (dry weight of total Kjeldahl nitrogen as percent of dry leaf weight) > 3.2 percent. They also found that the minimum number of eggs deposited on a plant increased with increasing canopy diameter, leaf moisture, and/or leaf nitrogen above these threshold values, but the maximum number of eggs did not. During the study, eggs were detected on plants that did not meet all three criteria but with decreasing probability among plants with smaller canopies, lower leaf-water content, and/or lower leaf-nitrogen content. The minimum criteria for plant selection appeared to be canopy diameter > 1.0 m and leaf-nitrogen content > 2 percent (Wiesenborn and Pratt 2008). Nelson et al. (2014) in turn found that females will use smaller shrubs ("seedlings") when larger plants are not available so long as the shrubs exhibit suitable leaf conditions. Wiesenborn and Pratt (2008) suggest that the females

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

identify plants suitable for ovipositing based on visual cues such as the greenness of a plant, an indicator of leaf-nitrogen content (see also Nelson et al. 2015). Ongoing LCR MSCP studies are being conducted to test the feasibility of measuring leaf greenness as a way to quantify this indicator (S.M. Nelson 2015, personal communications). Nelson et al. (2015) also found that, with a very high statistical significance, females simply do not lay eggs on plants with more than a small percentage of dry leaves present, another indication of plant lushness. Wiesenborn and Pratt (2008) suggest that female selection of plants for ovipositing based on canopy diameter is a consequence of selection for plants with ample shade, which helps MNSW control their body temperature (Wiesenborn 1999). In turn, theoretically, the spacing of quailbush shrubs within a patch, and the overall size of the patch, would be expected to determine how widely MNSW adult females may search for suitable plants for ovipositing while avoiding exposure outside the canopies of the quailbush shrubs that comprise the patch. However, this topic has not been specifically studied.

Conversely, MNSW adult feeding/watering, hiding/resting, and mating behaviors affect the scientific study of MNSW by affecting adult visibility within the quailbush shrub canopy. Although these proposed relationships have not been formally studied, their existence and importance are well documented. The literature on MNSW contains numerous descriptions of MNSW field study methods and frequent comments about the difficulties of monitoring MNSW in the field. These difficulties arise specifically because of the way MNSW adults mostly remain within the quailbush canopy and are most visible only when patrolling or flying to and from nectar sources. The literature also documents searches for alternative monitoring methods such as eDNA (Nelson et al. 2015) that bypass the need to directly observe MNSW individuals in order to assess their abundance and spatial distribution.

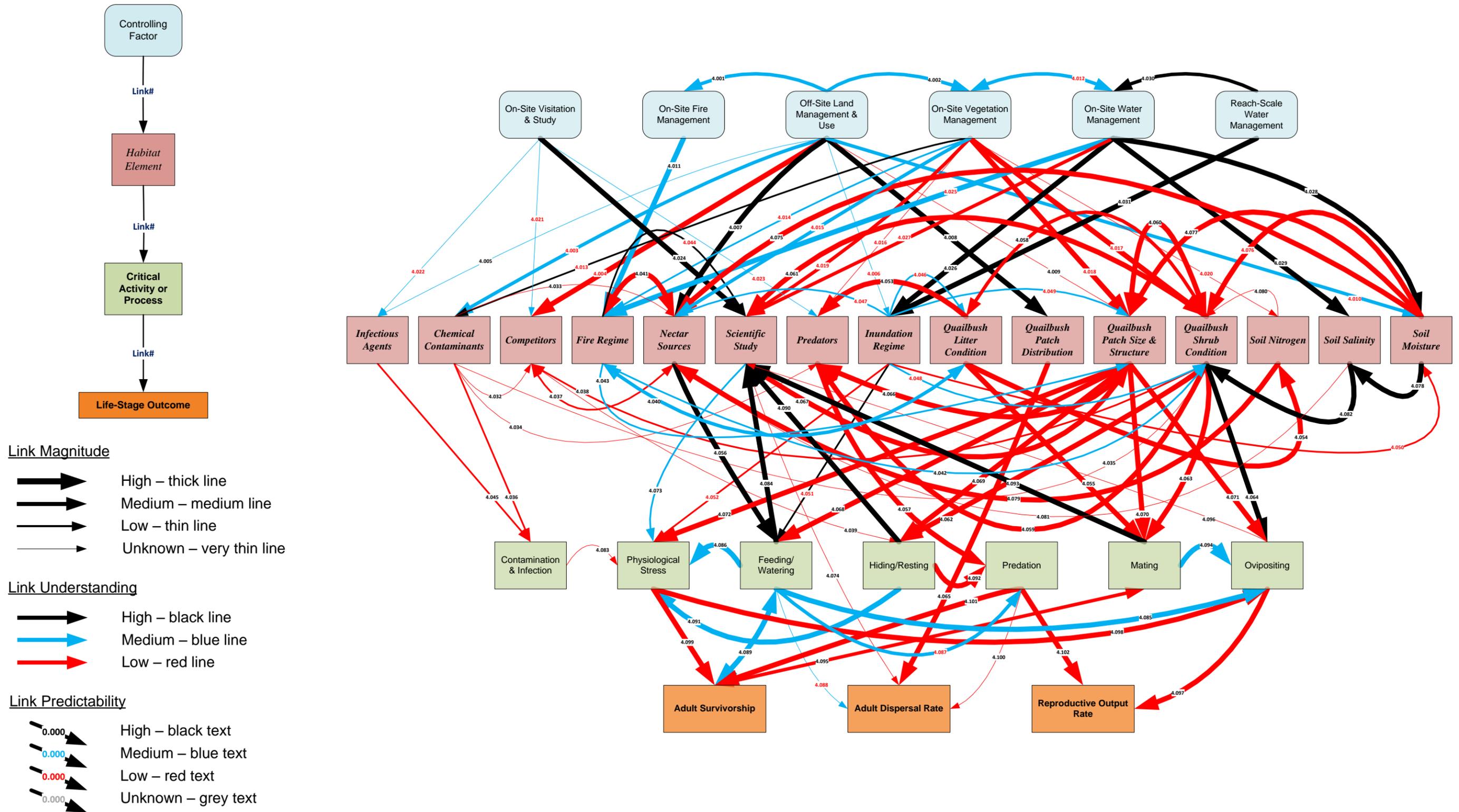


Figure 11.—MNSW Life Stage 4 – Adult Stage, complete model.

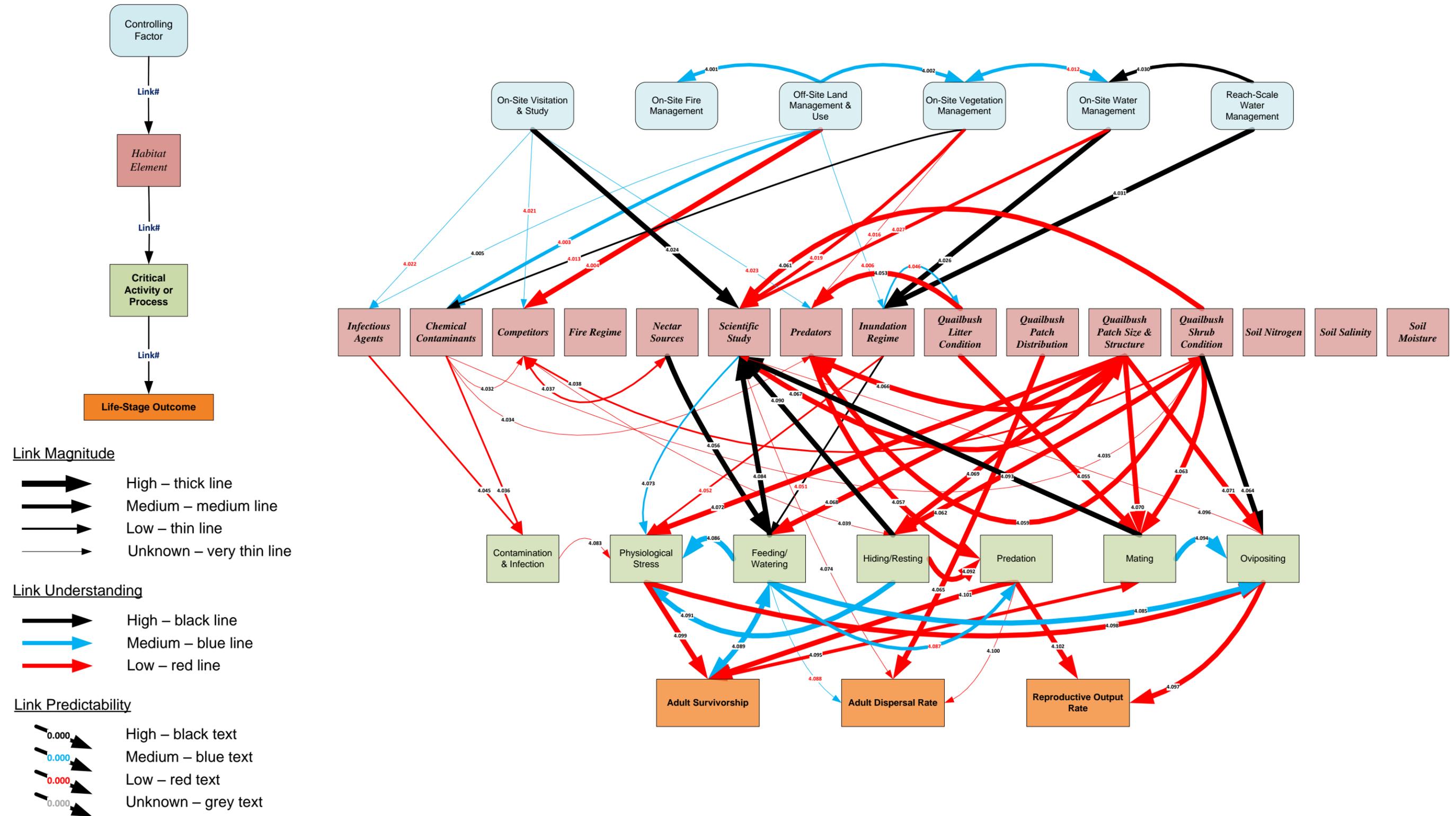


Figure 12.—MNSW Life Stage 4 – Adult Stage, omitting links that affect only quailbush or nectar source ecology.

# Chapter 7 – Causal Relationships Across All Life Stages

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

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

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

Five of the seven critical biological activities and processes identified in the CEM (chapter 3) have direct influences on one or more of the six life-stage outcomes across the four MNSW life stages. Table 7 shows which critical activities and processes directly affect each life-stage outcome. Each relationship between a critical biological activity and process and a life-stage outcome is color coded to indicate the magnitude (**High**, **Medium**, **Low**, **Unknown**) of the relationship. Two critical biological activities and processes have no direct effect on any life-stage outcomes.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 7.—Direct effects of critical biological activities and processes on life-stage outcomes (number of life stages in which relationship occurs)

Life-stage outcomes →	Egg survivorship	Larval survivorship	Pupal survivorship	Adult survivorship	Adult dispersal rate	Reproductive output rate
Critical biological activities and processes ↓						
Contamination and infection						
Feeding/watering		1		1	1	
Hiding/resting						
Mating				1		
Ovipositing						1
Physiological stress	1	1	1	1		
Predation	1	1	1	1	1	1

Table 7 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities and processes on life-stage outcomes:

- Feeding/watering activities and their rates of success are proposed to directly affect larval and adult survivorship, with high magnitude, and to affect the adult dispersal rate, with unknown magnitude.
- Mating activity is proposed to directly affect adult survivorship, with medium magnitude. This activity also affects life-stage outcomes indirectly, through its effects on ovipositing activity, as discussed below.
- Ovipositing affects the reproductive output rate, with high magnitude.
- Physiological stress is proposed to directly affect survivorship in all four life stages, with high magnitude.
- Predation is proposed to directly affect all six life-stage outcomes, affecting survivorship in all four life stages and the reproductive output rate, with high magnitude, and to affect the adult dispersal rate, with unknown magnitude.

## EFFECTS OF CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES ON EACH OTHER

Several critical biological activities and processes help shape other critical biological activities and processes, thereby influencing life-stage outcomes indirectly across the four MNSW life stages. Table 8 shows the number of life stages in which each critical biological activity and process directly affects one or more other critical biological activities and processes and the average magnitudes of these effects. Each relationship between one critical biological activity and process and another is again color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship.

Table 8.—Direct effects of critical biological activities and processes on other critical biological activities and processes (number of life stages in which relationship occurs)

Affected critical biological activity and process →	Contamination and infection	Feeding/watering	Hiding/resting	Mating	Ovipositing	Physiological stress	Predation
Causal critical biological activity and process ↓	Contamination and infection	Feeding/watering	Hiding/resting	Mating	Ovipositing	Physiological stress	Predation
Contamination and infection						4	
Feeding/watering					1	2	2
Hiding/resting						3	3
Mating					1		
Ovipositing							
Physiological stress					1		
Predation							

One critical biological activity, contamination and infection, is proposed as a possible causal agent affecting physiological stress levels in all four life stages, but with unknown magnitude. Two critical activities, ovipositing and predation,

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

have no direct effects on any other critical biological activity and process. Four critical activities or processes – contamination and infection, feeding/watering, hiding/resting, and mating – are not directly affected by any other critical activities or processes.

Table 8 indicates the following important (medium- or high-magnitude) direct effects of critical biological activities and processes on other critical biological activities and processes:

- Feeding/watering activities are proposed to affect the rate of ovipositing in the adult life stage, with high magnitude; to affect the rate of physiological stress in the larval and adult life stages, with high magnitude; and to affect the rate of predation in the larval and adult life stages, with medium magnitude.
- Hiding/resting activities are proposed to affect the rates of physiological stress and predation in the pupal, larval, and adult life stages, with high magnitude.
- The rates of mating and physiological stress are both proposed to affect the rate of ovipositing in the adult life stage, with high magnitude.

Table 8 also indicates that contamination and infection may result in physiological stress in all four life stages but with unknown magnitude.

## **EFFECTS OF HABITAT ELEMENTS ON CRITICAL BIOLOGICAL ACTIVITIES AND PROCESSES**

The 15 habitat elements identified in the CEM (chapter 4) have similar direct influences on the 7 critical biological activities and processes (chapter 3) across all MNSW life stages. Table 9 shows the number of life stages in which each habitat element directly affects one or more critical biological activities and processes. Table 9 identifies each habitat element by its short label. Chapter 4 provides the full name for each element. Each relationship between a habitat element and a critical biological activity and process in table 9 is color coded to indicate the average magnitude (**High**, **Medium**, **Low**, **Unknown**) of the relationship.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 9.—Direct effects of habitat element on critical biological activities and processes (number of life stages in which relationship occurs)

Affected critical biological activities and processes →	Contamination and infection	Feeding/watering	Hiding/resting	Mating	Ovipositing	Physiological stress	Predation	Grand total
Causal habitat element ↓								
Chemical contaminants	4							4
Competitors			2					2
Fire regime								
Infectious agents	4							4
Inundation regime		2				4		6
Nectar sources		1						1
Predators							4	4
Quailbush litter condition			2	1				3
Quailbush patch distribution								
Quailbush patch size and structure		1	1	1	1	4		8
Quailbush shrub condition		1	2	1	1	3	1	9
Scientific study						4		4
Soil moisture								
Soil nitrogen								
Soil salinity								

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 9 indicates the following direct effects of habitat elements on critical biological activities and processes:

- Five habitat elements have no direct effects on any critical biological activities and processes: fire regime, quailbush patch distribution, soil moisture, soil nitrogen, and soil salinity. These five affect critical biological activities and processes only indirectly by affecting other habitat elements with direct impacts on critical biological activities and processes as discussed below.
- Both chemical contaminants and infectious agents are proposed to affect the rate of contamination and infection in all four life stages, but with low magnitude.
- Competitors are proposed to affect hiding/resting activity in the larval and adult life stages, but with unknown magnitude.
- The inundation regime is proposed to affect feeding/watering activities in the larval and adult life stages, with low magnitude, and to affect physiological stress in all four life stages, with low magnitude.
- Nectar sources affect feeding/watering activities in the adult life stage, with high magnitude.
- Predators affect the rate of predation in all four life stages, with high magnitude.
- Quailbush litter condition affects hiding/resting activities in the larval and pupal life stages, and mating activities in the adult life stage, all with high magnitude.
- Quailbush patch size and structure is proposed to affect feeding/watering activities, hiding/resting activities, mating, and ovipositing in the adult life stage, with high magnitude, and to affect physiological stress rates in all four life stages, also with high magnitude.
- Quailbush shrub condition affects feeding/watering activities in the larval life stage; hiding/resting activities in the larval and adult life stages; mating and ovipositing in the adult life stage; and physiological stress in the egg, larval, and pupal life stages. All of these effects are proposed to have high magnitude. Additionally, quailbush shrub condition is proposed to affect predation on MNSW eggs, but with unknown magnitude.

**MacNeill’s Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

- Scientific study is proposed to affect physiological stress in all four life stages, but with low magnitude.
- Quailbush patch size and structure and quailbush shrub condition are identified as affecting the greatest number of critical activities and processes across the greatest number of life stages.
- Nectar sources, predators, quailbush litter condition, quailbush patch size and structure, and quailbush shrub condition are proposed to consistently affect one or more critical activities or processes in one or more life stages, with high magnitude. As noted throughout chapters 3, 4, and 6, however, very little is known about the ways in which predators and quailbush litter condition affect MNSW.
- As noted earlier, one habitat element affects a life-stage outcome directly rather than through effects on critical biological activities and processes. Specifically (see chapter 6, “MNSW Life Stage 4 – Adult Stage”), quailbush patch distribution directly affects the adult dispersal rate, with high magnitude but low understanding.

## **EFFECTS OF HABITAT ELEMENTS ON EACH OTHER**

Several habitat elements help shape other habitat elements, thereby influencing critical biological activities and processes indirectly across all MNSW life stages. Table 10 shows the number of life stages in which each habitat element directly affects one or more other habitat elements and the average magnitudes of these effects. Table 10 identifies each habitat element by its short label. Chapter 4 provides the full name for each element. Each relationship between a habitat element and another is again color coded to indicate the average magnitude (**High**, **Medium**, **Low**, **Unknown**) of the relationship. A bold-faced, italicized value (e.g., ***1***) indicates that a relationship is bi-directional (reciprocal). Five habitat elements have no direct effect on any other habitat elements included in the CEM, and five habitat elements are not affected by any other habitat elements.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 10.—Direct effects of habitat elements on other habitat elements (number of life stages in which relationship occurs)

Affected habitat element →	Chemical contaminants	Competitors	Fire regime	Infectious agents	Inundation regime	Nectar sources	Predators	Quailbush litter condition	Quailbush patch distribution	Quailbush patch size and structure	Quailbush shrub condition	Scientific study	Soil moisture	Soil nitrogen	Soil salinity	Grand total
Causal habitat element ↓	Chemical contaminants	Competitors	Fire regime	Infectious agents	Inundation regime	Nectar sources	Predators	Quailbush litter condition	Quailbush patch distribution	Quailbush patch size and structure	Quailbush shrub condition	Scientific study	Soil moisture	Soil nitrogen	Soil salinity	Grand total
Chemical contaminants		2				1	4				4					11
Competitors						1					2					3
Fire regime						1		3		4	4	4				16
Infectious agents																0
Inundation regime						1		3		4	4		4			16
Nectar sources																0
Predators																0
Quailbush litter condition								3							3	6
Quailbush patch distribution																0
Quailbush patch size and structure								4				4				8
Quailbush shrub condition								4	3	4	4					15
Scientific study																0
Soil moisture						1				4	4				4	13
Soil nitrogen						1					4					5
Soil salinity						1					4					5

Note: ***Bold-faced italics*** indicates a bi-directional (reciprocal) relationship.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 10 indicates the following direct effects of habitat elements on other habitat elements proposed in the CEM:

- Chemical contaminants are hypothesized to affect competitors in the larval and adult life stages, nectar sources in the adult life stage, and predators and quailbush shrub condition in all four life stages, but with unknown magnitude.
- Competitors are hypothesized to affect nectar sources for the adult life stage and quailbush shrub condition for the larval and adult life stages, and vice versa, with low magnitude.
- The fire regime is hypothesized to affect nectar sources for the adult life stage, and vice versa, with high magnitude; quailbush litter condition for the larval, pupal, and adult life stages, and vice versa, with medium magnitude; quailbush patch size and structure and scientific study in all four life stages, with low low magnitude, and quailbush shrub condition for all four life stages, and vice versa, with low magnitude. Fire can affect scientific study, destroying study sites that are undergoing long-term study. On the other hand, the edges of burned areas also can provide clear lines of sight for observing MNSW.
- The inundation regime is hypothesized to affect nectar sources for the adult life stage; quailbush litter condition for the larval, pupal, and adult life stages; and quailbush patch size and structure, quailbush shrub condition, and soil moisture for all four life stages. All these effects of the inundation regime are rated low for magnitude.
- Quailbush litter condition is hypothesized to affect predators and soil nitrogen for the larval, pupal, and adult life stages, with high magnitude.
- Quailbush patch size and structure is hypothesized to affect the pool of predators (what types of predators are present, in what numbers) for all life stages, with high magnitude. It is also hypothesized to affect scientific study, and vice versa, with high magnitude for all life stages. These latter interactions occur because patch size and structure affect the ability of observers to detect MNSW in any life stage within the quailbush canopy. Conversely, field observers may alter patch size and structure intentionally to facilitate observation.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

- Quailbush shrub condition is hypothesized to affect predators for all life stages, with high magnitude; quailbush litter condition for the larval, pupal, and adult life stages, with medium magnitude; and quailbush patch size and structure for all life stages, and vice versa, with high magnitude. Additionally, quailbush shrub condition is hypothesized to affect scientific study of all life stages, with high magnitude. Shrub condition affects the ability of observers to detect MNSW in any life stage within the canopy of individual shrubs.
- Soil moisture affects nectar sources for the adult life stage, with high magnitude, and affects quailbush patch size and structure, quailbush shrub condition, and soil salinity for all four life stages, with high magnitude.
- Soil nitrogen affects nectar sources for the adult life stage, with high magnitude, and is hypothesized to affect quailbush shrub condition for all life stages, but with unknown magnitude.
- Finally, soil salinity is hypothesized to affect nectar sources for the adult life stage, but with unknown magnitude, and to affect quailbush shrub condition for all life stages, with high magnitude.

A comparison of tables 9 and 10 provides additional information on the small number of habitat elements that strongly, directly affect critical biological activities and processes. As noted above for table 9, this small number of pivotal habitat elements consists of quailbush patch size and structure, quailbush shrub condition, nectar sources, predators, and quailbush litter condition. Table 10 indicates that these five habitat elements, in turn, are affected by other habitat elements as follows:

- Quailbush patch size and structure is most strongly affected by the condition of individual quailbush shrubs and by soil moisture.
- Quailbush shrub condition is most strongly affected by soil moisture and soil salinity.
- Nectar sources are hypothesized to be most strongly affected by the fire regime, soil moisture, and soil nitrogen.
- Predators are hypothesized to be most strongly affected by quailbush litter condition, quailbush shrub condition, and quailbush patch size and structure.
- Quailbush litter condition is hypothesized to be most strongly affected by the fire regime and quailbush shrub condition.

## EFFECTS OF CONTROLLING FACTORS ON HABITAT ELEMENTS

The six controlling factors discussed in chapter 5 have the same direct effects on the same habitat elements across all life stages. Table 11 shows the magnitudes of direct influence of the controlling factors on the 15 habitat elements identified in the CEM. Each relationship indicated in table 11 is color coded to indicate the average magnitude (High, Medium, Low, Unknown) of the relationship. None of the relationships in table 11 are reciprocal (bi-directional).

Table 11.—Direct effects of controlling factors on habitat elements (number of life stages in which relationship occurs)

Affected habitat element →	Causal controlling factor ↓														
	Chemical contaminants	Competitors	Fire regime	Infectious agents	Inundation regime	Nectar sources	Predators	Quailbush litter condition	Quailbush patch distribution	Quailbush patch size and structure	Quailbush shrub condition	Scientific study	Soil moisture	Soil nitrogen	Soil salinity
Offsite land management and use	4	2		4	4	1			1	4			4		
Onsite fire management			4												
Onsite vegetation management	4		4			1	4			4	4	4		4	
Onsite visitation and study		2		4			4					4			
Onsite water management			4		4							4	4		4
Reach-scale water management					4										

One habitat element, quailbush litter condition, is not directly affected by any of the six controlling factors. Controlling factors affect competitors for only two life stages (larval and adult) and affect nectar sources for only one life stage (adult). Otherwise, the six controlling factors affect the indicated habitat elements for all four MNSW life stages.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 11 indicates the following direct effects of controlling factors on habitat elements proposed in the CEM:

- Offsite land management and use affects competitors within MNSW habitat sites for both the larval and adult life stages, nectar sources for the adult life stage, quailbush patch distribution for adult dispersal, and quailbush patch size and structure for all four life stages, all with high magnitude. Offsite land management and use affects chemical contaminants and soil moisture within MNSW habitat sites for all four life stages, with medium magnitude, and affects infectious agents and the inundation regime within MNSW habitat sites for all four life stages with unknown magnitude.
- Onsite fire management affects the fire regime within MNSW habitat sites, with high magnitude.
- Onsite vegetation management affects quailbush patch size and structure and quailbush shrub condition within MNSW habitat sites for all life stages, with high magnitude, and nectar sources for the adult stage, with medium magnitude. It also affects the scientific study of all four life stages within MNSW habitat sites, with medium magnitude, by affecting the ability of field crews to detect and observe in all four life stages. Onsite vegetation management also is hypothesized to affect chemical contamination and the fire regime within MNSW habitat sites for all life stages, with low magnitude. Finally, onsite vegetation management is hypothesized to have the potential to affect predators and soil nitrogen within MNSW habitat sites for all four life stages, but with unknown magnitude.
- Onsite visitation and study is hypothesized to have the potential to affect competitors for the larval and adult life stages, and infectious agents and predators for all life stages within MNSW habitat sites, with unknown magnitude.
- Onsite water management affects the fire and inundation regimes, soil moisture, and soil salinity within MNSW habitat sites for all life stages, with high magnitude, and scientific study for all life stages, with medium magnitude. The latter relationship arises because onsite water applications may create linear wetted zones along ditches that provide clear lines of sight for observing MNSW.
- Finally, reach-scale water management affects the inundation regime within MNSW habitat sites for all life stages, with high magnitude.

## POTENTIALLY INFLUENTIAL CAUSAL RELATIONSHIPS WITH LOW UNDERSTANDING

Many causal relationships proposed in the CEM (see chapter 6) are rated as having low understanding. The CEM proposes these relationships based on established ecological principles, information on butterflies or skippers in general, suggestions in the literature on MNSW, and suggestions from experts consulted for this CEM. However, few or no studies directly address or assess these potential causal relationships. As a result, the relationships are poorly understood.

Tables 12–14 identify those causal relationships that the CEM proposes have high magnitude but low understanding. Table 12 identifies such relationships specifically in which the causal agent is a controlling factor; table 13 identifies such relationships in which the causal agent is a habitat element; and table 14 identifies such relationships in which the causal agent is a critical biological activity and process. Tables 12–14 indicate the number of life stages for which the CEM proposes the relationship. A bold-faced, italicized value (e.g., ***1***) indicates that a relationship is bi-directional (reciprocal).

Table 12.—High-magnitude but poorly understood relationships between habitat elements and other variables (number of life stages in which relationship occurs)

Affected habitat element →	Competitors	Quailbush patch size and structure	Quailbush shrub condition
Causal controlling factor ↓			
Offsite land management and use	<b>2</b>		
Onsite vegetation management		<b>4</b>	<b>4</b>

Table 12 identifies 10 links across the four life stages, with a controlling factor as the causal agent rated as having high magnitude but low understanding. All 10 relationships involve effects of controlling factors on habitat elements. The relationships concern:

- The potential effects of offsite land management and use on the array of species that can occur within MNSW habitat sites and compete with MNSW for food materials and/or physical habitat.
- The potential effects of onsite vegetation management practices on quailbush patch size and structure and quailbush shrub condition.

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 13.—High-magnitude but poorly understood relationships between habitat elements and other variables (number of life stages in which relationship occurs)

Affected life-stage outcome, critical biological activity and process, or habitat element →	Adult dispersal rate	Feeding/watering	Hiding/resting	Mating	Nectar sources	Ovipositing	Physiological stress	Predation	Predators	Quailbush patch size and structure	Quailbush shrub condition	Scientific study	Soil nitrogen
Fire regime					<b>1</b>								
Predators								<b>4</b>					
Quailbush litter condition			<b>2</b>	<b>1</b>					<b>3</b>				<b>3</b>
Quailbush patch distribution	<b>1</b>												
Quailbush patch size and structure		<b>1</b>	<b>1</b>	<b>1</b>		<b>1</b>	<b>4</b>		<b>4</b>				<b>4</b>
Quailbush shrub condition			<b>2</b>	<b>1</b>			<b>3</b>		<b>4</b>	<b>4</b>			<b>4</b>
Soil moisture					<b>1</b>					<b>4</b>	<b>4</b>		
Soil nitrogen					<b>1</b>								

Note: ***Bold-faced italics*** indicates a bi-directional (reciprocal) relationship.

Table 13 identifies 59 links across the four life stages, with a habitat element as the causal agent rated as having high magnitude but low understanding. The 59 include 1 direct effect on a life-stage outcome, 21 effects on critical biological activities and processes, and 37 effects on other habitat elements. Nine of the relationships are bi-directional (i.e., involve reciprocal causation). The 59 relationships concern:

- The ways in which the fire regime may affect the types and abundances of nectar sources available in and around MNSW habitat sites and conversely how the types and abundances of nectar sources available in and around MNSW habitat sites may affect the local fire regime.
- The potential effects of the predator pool – what potential predator species are present in MNSW habitat sites, in what numbers, etc. – on predation of MNSW in all four life stages.
- The potential effects of quailbush litter condition on larval and pupal hiding/resting success, adult mating behaviors, the array of species present that may prey on MNSW within and beneath the quailbush canopy, and soil nitrogen levels.

**MacNeill’s Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

- The potential effects of quailbush patch distribution on the adult dispersal rate.
- The potential effects of quailbush patch size and structure on adult feeding/watering, hiding/resting, mating, and ovipositing; on physiological stress levels in all four life stages; on the array of species present that may prey on MNSW within and above the quailbush canopy; and the potential reciprocal interactions between quailbush patch size and structure and the effectiveness of various methods of field detection and observation in the study of MNSW.
- The potential effects of quailbush shrub condition on larval and adult hiding/resting success, adult mating, physiological stress for the egg through pupal life stages, the array of species present that may prey on MNSW within and above the quailbush canopy, the effectiveness of various methods of field detection and observation in the study of MNSW, and the potential reciprocal interactions between quailbush shrub condition and quailbush patch size and structure.
- The potential effects of soil moisture and soil nitrogen on the types and abundances of nectar sources available in and around MNSW habitat sites.
- The potential effects of soil moisture on quailbush patch size and structure and quailbush shrub condition.

Table 14.—High-magnitude but poorly understood relationships between critical biological activities and processes and other variables (number of life stages in which relationship occurs)

<b>Affected life-stage outcome or critical biological activity and process →</b>								
	<b>Adult survivorship</b>	<b>Egg survivorship</b>	<b>Larval survivorship</b>	<b>Ovipositing</b>	<b>Physiological stress</b>	<b>Predation</b>	<b>Pupal survivorship</b>	<b>Reproductive output rate</b>
<b>Causal critical biological activity and process ↓</b>								
Feeding/watering					1			
Hiding/resting					1	3		
Ovipositing								1
Physiological stress	1	1	1	1			1	
Predation	1	1	1				1	1

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

Table 14 identifies 15 links across the four life stages, with a critical biological activity and process as the causal agent rated as having high magnitude but low understanding. The 15 include 9 direct effects on life-stage outcomes and 6 direct effects on other critical biological activities and processes. None of the 15 relationships are bi-directional (i.e., involve reciprocal causation). The 15 relationships concern:

- The potential effects of feeding/watering activities and success rates on larval physiological stress.
- The potential effects of hiding/resting activities and success rates on larval physiological stress and on the rates of predation experienced by MNSW larvae, pupae, and adults.
- The potential effects of ovipositing activities and success rates on the MNSW reproductive rate.
- The potential effects of physiological stress rates on survivorship in all four life stages and on ovipositing activities and success rates.
- The potential effects of predation on survivorship in all four life stages.

## Chapter 8 – Discussion and Conclusions

This document presents a CEM for the MNSW, a butterfly. The purpose of this model is to help LCR MSCP personnel identify areas of scientific certainty versus uncertainty concerning MNSW ecology, the effects of specific stressors, the effects of specific management actions aimed at habitat and species restoration, and the indicators used to measure MNSW habitat and population conditions.

The model addresses the MNSW population along the flood plain of the LCR. Specifically, the model addresses MNSW within the conservation areas along the LCR that currently provide or could provide MNSW habitat under the HCP. The CEM methodology involves 6 core steps:

1. For each species, identify the **life stages** that need to be distinguished, each with its own suite of ecological processes and environmental constraints.
2. For each life stage, identify the **life-stage outcomes** of concern – generally survivorship – and also reproductive output where appropriate.
3. For each life-stage outcome, identify the **critical biological activities and processes**, the rates of which shape the rates for the life-stage outcomes. These critical biological activities and processes include basic ecological processes, such as competition and predation, as well as life-stage-specific activities such as drifting or spawning.
4. For each critical biological activity and process, identify the critical **habitat elements**. These consist of features of the physical and biological environment, the abundance, composition, or other properties of which shape the rates of critical biological activities and processes. Examples can include the abundance and composition of the assemblages of potential predators or competitors.
5. Identify **controlling factors**, consisting of human activities and environmental drivers, which shape the abundance and/or condition of each habitat element. The model omits factors outside the geographic or temporal scope of control of the LCR MSCP, such as climate change.

**MacNeill's Sootywing Skipper (*Hesperopsis gracieae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

6. Identify potential **causal relationships** among these model components and rate these proposed relationships in terms of their apparent or likely magnitude, predictability, and level of understanding in the scientific literature. The identification and rating of the causal relationships rests on established ecological principles, studies of Colorado River ecology and hydrology in general, studies of MNSW ecology across the Colorado River basin in general, and studies of MNSW within the LCR in particular.

The MNSW conceptual ecological model identifies four life stages: egg, larval, pupal, and adult. Life-stage outcomes consist of the survival rate for each life stage, the adult reproductive participation rate, and rate of adult dispersal. The CEM identifies seven critical biological activities and processes that affect one or more of these life-stage outcomes: contamination and infection, feeding/watering, hiding/resting, mating, ovipositing, physiological stress, and predation.

In turn, the CEM identifies 15 habitat elements, the abundance, composition, or other properties of which affect one or more critical activities or processes: chemical contaminants, competitors, fire regime, infectious agents, inundation regime, nectar sources, predators, quailbush litter condition, quailbush patch distribution, quailbush patch size and structure, quailbush shrub condition, scientific study, soil moisture, soil nitrogen, and soil salinity.

Finally, the CEM identifies six controlling factors, the dynamics of which affect the abundance, composition, or other properties of one or more habitat elements: offsite land management and use, onsite fire management, onsite vegetation management, onsite visitation and study, onsite water management, and reach-scale water management.

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

- Three controlling factors – offsite land management and use, onsite vegetation management, and onsite water management – have consistently high-magnitude effects on multiple habitat elements across all life stages. Onsite fire management and reach-scale water management have high-magnitude effects on a single habitat element each, the fire regime and the inundation regime, respectively.
- Two habitat elements – quailbush patch size and structure and quailbush shrub condition – have consistently high-magnitude effects on multiple critical biological activities and processes across all life stages. Quailbush litter condition affects two critical biological activities and processes across two life stages. The potential array of predator species present in

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

MNSW habitat sites and their numbers affects one critical biological process – predation – in all four life stages. The types, abundances, and spatial and temporal distributions of nectar sources strongly affect adult feeding/watering success.

- Seven habitat elements have high-magnitude direct effects on other habitat elements and thereby strongly *indirectly* affect one or more critical biological activities and processes across one or more MNSW life stages. Specifically, the fire regime strongly affects nectar sources; quailbush litter condition strongly affects the potential array of predator species present in MNSW habitat sites and their numbers and also may strongly affect soil nitrogen; quailbush patch size and structure and quailbush shrub condition strongly affect each other and both strongly affect the potential array of predator species present in MNSW habitat sites and their numbers; soil moisture strongly affects nectar sources, quailbush patch size and structure, quailbush shrub condition, and soil salinity; soil nitrogen strongly affects nectar source conditions; and soil salinity strongly affects quailbush shrub condition.
- Four critical biological activities potentially strongly affect life-stage outcomes in one or more life stages. Physiological stress and predation potentially strongly affect survivorship in all four life stages. Predation also potentially strongly affects adult reproductive output. Feeding/watering activities and their success are proposed to strongly affect survivorship among both larvae and adults, and ovipositing activities and their success necessarily affect reproductive output.
- Four critical biological activities and processes have high-magnitude direct effects on other critical biological activities and processes and thereby strongly *indirectly* affect one or more life-stage outcomes across the MNSW life cycle. Specifically, feeding/watering activities and their success potentially strongly affect ovipositing and the rates of physiological stress among larvae and adults; hiding/resting activities and their success potentially strongly affect both predation and physiological stress among pupae, larvae, and adults; and both mating activities and their success and rates of physiological stress affect ovipositing among adults.

The assessment of causal relationships also identified those with high magnitude but low understanding. Two controlling factors – offsite land management and use and onsite vegetation management – have high-magnitude but poorly understood impacts on habitat elements with significant cascading impacts on critical biological activities and processes. Eight habitat elements – fire regime, predators, quailbush litter condition, quailbush patch distribution, quailbush patch

**MacNeill's Sootywing Skipper (*Hesperopsis graciellae*) (MNSW)  
Basic Conceptual Ecological Model for the Lower Colorado River**

size and structure, quailbush shrub condition, soil moisture, and soil nitrogen – have numerous high-magnitude but poorly understood impacts on other habitat elements, on critical biological activities and processes, and in one case, directly on a life-stage outcome.

Life-stage outcomes, critical biological activities and processes, and habitat elements may also be shaped by other causal relationships, about which there is not sufficient information to assess link magnitude. Tables 7–11, in chapter 7, all show one or more hypothesized causal relationships with unknown magnitude. The CEM proposes the existence of these relationships based on established ecological principles, information on butterflies or skippers in general, suggestions in the literature on MNSW, or suggestions from experts consulted for this CEM. However, too little is known about these relationships to form hypotheses about link magnitude.

The CEM for MNSW thus, in part, highlights aspects of the ecology of the species already well established or the subjects of established research programs. These topics include the close relationships of MNSW ecological dynamics to the ecological dynamics of quailbush, and an array of nectar sources, and the possible relationships of these dynamics to soil conditions. Additionally, the CEM highlights numerous aspects of MNSW ecology that are less well studied but that likely also play significant roles in shaping the abundance and distribution of MNSW within individual habitat patches and across the LCR as a whole. Finally, the CEM highlights aspects of MNSW ecology that, while potentially significant, are too little studied to allow any inferences concerning their importance.

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 MNSW. 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.

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# **ATTACHMENT 1**

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

# OVERVIEW OF METHODOLOGY

The conceptual ecological models (CEMs) for species covered by the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) Habitat Conservation Plan expand on a methodology developed by the Sacramento-San Joaquin Delta Ecosystem Restoration Program (ERP): [https://www.dfg.ca.gov/ERP/conceptual\\_models.asp](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 and 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 cover, 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 and process
- (5) The effect of one critical biological activity and process on another
- (6) The effect of a critical biological activity and 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 and 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 and process on a particular life-stage outcome may depend on the effects of several habitat elements on that critical biological activity and 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 and 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)

<b>Link intensity</b> – 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)

<b>Link spatial scale</b> – 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)

<b>Link temporal scale</b> – 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

<b>Link magnitude</b> – 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 $\geq 2.67$
Medium	Numerical average $\geq 1.67$ 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)

<b>Link predictability</b> – 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)

<b>Understanding</b> – 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 and 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 and process, or life-stage outcome.
G	Effect Node	Identifies the effect node in the link.
H	Link Reason	States the rationale for including the link in the conceptual ecological model, including citations as appropriate.
I	Link Character Type	Identifies the character of the link based on standard definitions.
J	Link Character Direction	Identifies whether the link is uni- or bi-directional.
K	Link Character Reason	States the rationale for the entries for Link Character Type and Link Character Direction, including citations as appropriate.
L	Link Intensity	Shows the rating of link intensity based on the definitions in table 1-1.
M	Link Spatial Scale	Shows the rating of link spatial scale based on the definitions in table 1-2.
N	Link Temporal Scale	Shows the rating of link temporal scale based on the definitions in table 1-3.
O	Link Average Magnitude	Shows the numerical average rating of link intensity, spatial scale, and temporal scale based on the definitions in table 1-4.
P	Link Magnitude Rank	Shows the overall rating of link magnitude based on the Link Average Magnitude, grouped following the criteria in table 1-4.
Q	Link Magnitude Reason	States the rationale for the ratings for link intensity, spatial scale, and temporal scale, with citations as appropriate.
R	Link Predictability Rank	Shows the rating of link predictability based on the definitions in table 1-5.
S	Link Predictability Reason	States the rationale for the rating of link predictability, with citations as appropriate.
T	Link Understanding Rank	Shows the rating of link understanding based on the definitions in table 1-6.
U	Link Understanding Reason	States the rationale for the rating of link predictability, including comments on alternative interpretations and publications/experts associated with different interpretations when feasible, with citations as appropriate.
V	Management Questions	Briefly notes questions that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in knowledge concerning <i>management actions and options</i> , with reasoning, including the estimate of relative importance when possible.
W	Research Questions	Brief notes that appear to arise from the preceding entries for the link, focused on critical gaps or uncertainties in <i>basic scientific knowledge</i> , with reasoning, including the estimate of relative importance when possible.
X	Other Comments	Provides additional notes on investigator concerns, uncertainties, and questions.
Y	Update Status	Provides information on the history of editing the information on this link for updates carried out after completion of an initial version.

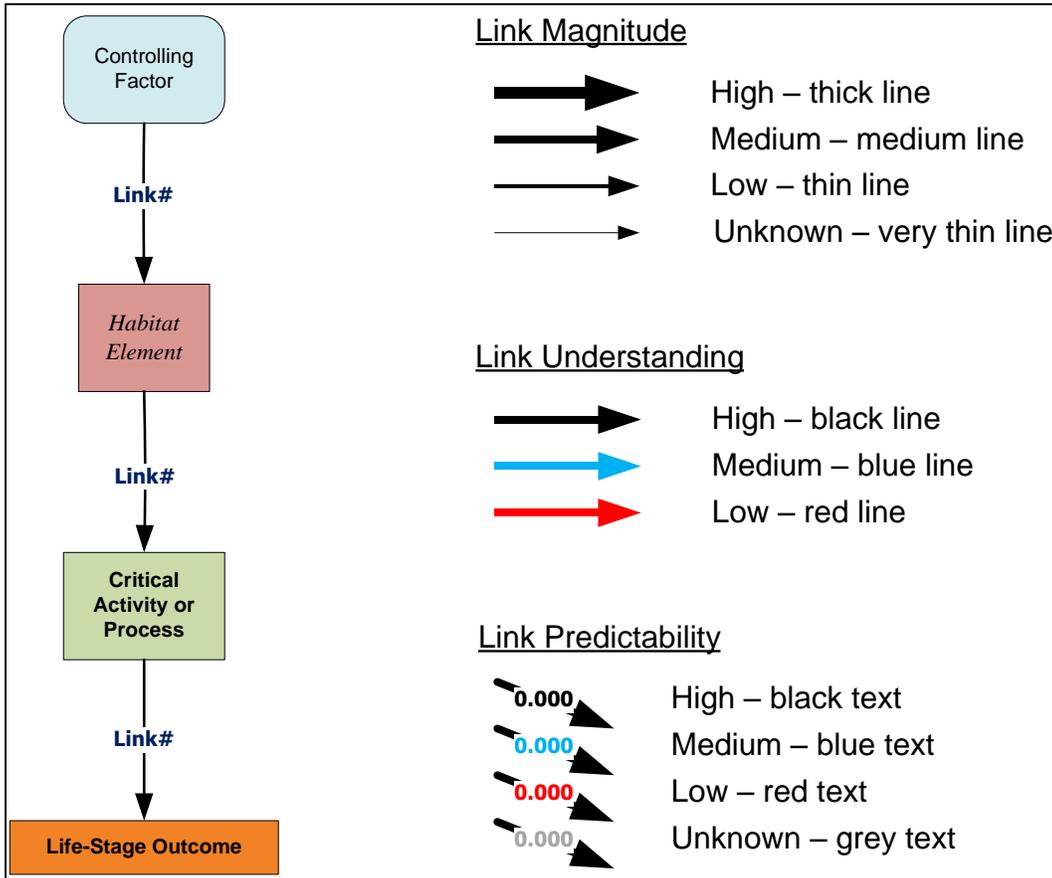


Figure 1-1.—Conventions for displaying cause and effect nodes, linkages, link magnitude, link understanding, and link predictability.

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