



# Lower Colorado River Multi-Species Conservation Program

*Balancing Resource Use and Conservation*

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

### 2018 Updates

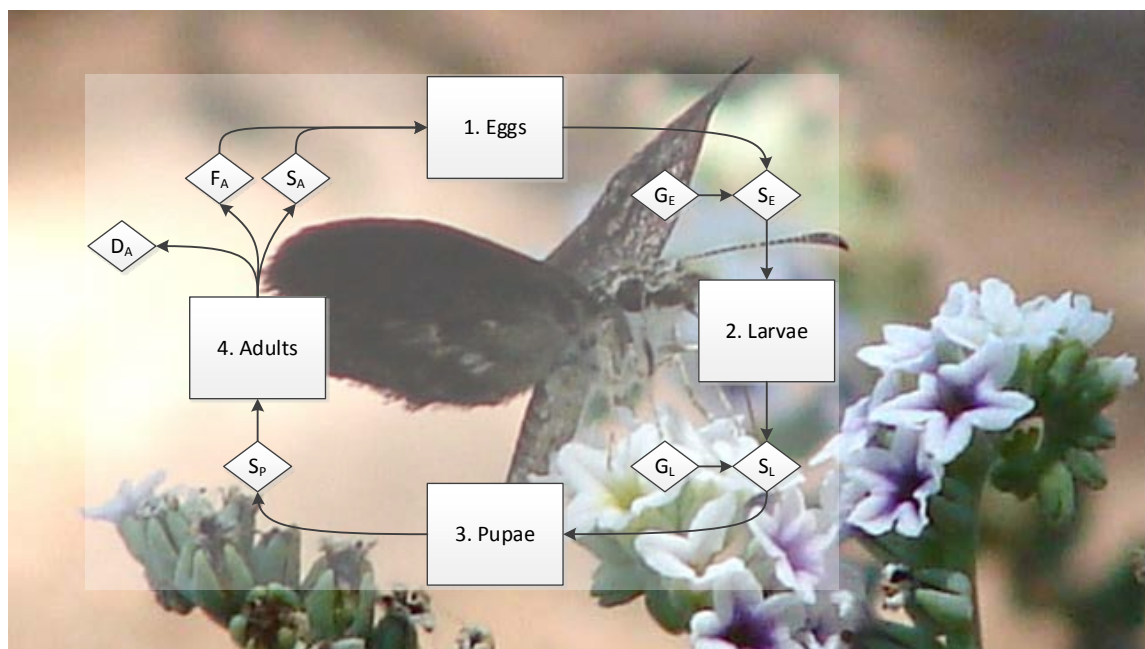


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April 2019

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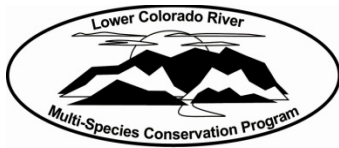
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# Lower Colorado River Multi-Species Conservation Program

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### 2018 Updates

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# ACRONYMS AND ABBREVIATIONS

CAP	critical activity or process
CEM	conceptual ecological model
CF	controlling factor
DNA	deoxyribonucleic acid
eDNA	environmental deoxyribonucleic acid
EPA	Environmental Protection Agency
LCR	lower Colorado River
LCR MSCP	Lower Colorado River Multi-Species Conservation Program
LSO	life-stage outcome
MNSW	MacNeill's sootywing skipper ( <i>Pholisora graciellae</i> = <i>Hesperopsis graciellae</i> [MacNeill])
Reclamation	Bureau of Reclamation
USDA	U.S. Department of Agriculture
USFHA	U.S. Federal Highway Administration

## Symbols

~	approximately
>	greater than
<	less than
%	percent

## DEFINITIONS

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

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

**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.

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## Foreword

This report provides an update to the original conceptual ecological model (CEM) prepared for the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) for the MacNeill's sootywing skipper (*Pholisora graciellae* = *Hesperopsis graciellae* [MacNeill]) (MNSW) (Braun 2015). It incorporates information reported in publications and presentations at professional meetings since the completion of the original MNSW conceptual ecological model, information from the professional experiences of LCR MSCP staff and other experts, and newer information on butterfly ecology more generally. An updated version of the CEM workbook incorporates the new information. This report constitutes an appendix to the original CEM. The full CEM report, including its life-stage diagrams, has not been updated.

The structure of this report (update) follows the structure of the original CEM report. Specifically, it presents and documents updates to chapters 1–6. It does not include updates to the original Executive Summary or chapters 7–8 because these sections were not updated.

This update changes the MNSW conceptual ecological model in several key respects. Three sets of changes are particularly noteworthy: (1) This update adds two new habitat elements, the “Herbaceous Vegetation Assemblage” and the “Woody Vegetation Assemblage” so that the CEM addresses crucial interactions of quailbush (*Atriplex lentiformis*) patches and MNSW with the larger vegetation communities of the lower Colorado River ecosystem. (2) This update also reclassifies competitors and predators under the two broad categories of arthropods and vertebrates so that the CEM better addresses crucial interactions of MNSW with the larger faunal communities of the lower Colorado River ecosystem. (3) This update reclassifies physiological stresses as mechanical and thermal stresses so that the CEM better addresses these crucial biological processes among MNSW. This update also adds egg growth and larval growth as life-stage outcomes. These four major sets of changes had cascading effects on the entire CEM.

This update also provides a list of all literature cited in the updates to chapters 1–6. In addition, it provides a list of all changes made to the name of the CEM components in order to standardize terminology across all CEMs.

This update both explicitly and implicitly identifies possible new research and monitoring questions concerning gaps in knowledge that may bear on adaptive management of MNSW. These questions may or may not reflect the current or future goals of LCR MCSP decisionmaking and are in no way meant as a call for the Bureau of Reclamation to undertake research to fill the identified knowledge gaps.

## Updates to Chapter 1 – Introduction

The information in paragraphs 4–6 in the initial section of chapter 1 is updated as follows:

MacNeill’s sootywing skippers (*Pholisora graciellae* = *Hesperopsis graciellae* [MacNeill]) (MNSW) do not occur along Las Vegas Wash, Nevada, despite their presence in the lower Muddy River Valley roughly 35 miles (56 kilometers) away (J. Eckberg 2018, personal communication; NatureServe 2018; Pratt and Wiesenborn 2011), the historic presence of MNSW within the Las Vegas metropolitan area, and the presence of herbaceous and woody vegetation assemblages along the wash that provide suitable habitat for MNSW (Andersen and Nelson 2013; Eckberg 2011, 2012, 2018; Nelson 2009; Nelson and Wydoski 2013; Scott 1986). The distance between Las Vegas Wash and the nearest population of MNSW, in the lower Muddy River Valley, may be too far for MNSW to cross without any intervening stepping-stone habitat. However, Eckberg (J. Eckberg 2018, personal communication) cautions, “... there have not been any surveys [along Las Vegas Wash] specific for this species and not many butterfly surveys in general.”

Reports on MNSW ecology and its status along the lower Colorado River (LCR) ecosystem that have appeared since completion of the original CEM (Braun 2015) include the Lower Colorado River Multi-Species Conservation Program (LCR MSCP) (2016), NatureServe (2018); Nelson et al. (2017), Wiesenborn (2017); and Davenport (2018). A revised version of Nelson et al. (2015) is in preparation (Nelson et al. 2018). Pratt et al. (2015) provide new information on MNSW genetic similarities to other butterfly species. Robinson et al. (2018), the U.S. Department of Agriculture (USDA), and the U.S. Federal Highway Administration (USFHA) (2017) and provide crucial new information on other Lepidoptera that may compete with MNSW through their use of quailbush (*Atriplex lentiformis*) or MNSW nectar sources as host plants.

Numerous recent publications on quailbush ecology, ecological effects of saltcedar (*Tamarix ramosissima*) biocontrol, and butterfly ecology in general also contribute to the present update. These additional publications include Eckberg and Rice (2016), Kennard et al. (2016), LoPresti (2016, 2017) on salt bladders on quailbush leaves; Bean and Dudley (2018), González et al. (2017a, 2017b), Nagler et al. (2017), Raynor et al. (2017), Sher et al. (2018), and Trathnigg and Phillips (2015) on the ecological effects of saltcedar biocontrol with and without active revegetation; and Gibbs et al. (2018), Rosa and Saastamoinen (2017), and Woestmann and Saastamoinen (2016) and on transgenerational effects of larval and adult diet restrictions in butterflies.

## CONCEPTUAL ECOLOGICAL MODEL PURPOSES

The present update does not propose any changes to this section of chapter 1. However, when the CEMs are fully updated, chapter 1 should be revised to indicate that the CEM methodology followed here is a crucial foundation for carrying out effects analyses, as described by Murphy and Weiland (2011, 2014) and illustrated by Jacobson et al. (2016).

## CONCEPTUAL ECOLOGICAL MODEL STRUCTURE

No change.

# Updates to Chapter 2 – MNSW Life Stage Model

## PROPOSED MNSW LIFE STAGES

The present update standardizes the names of the MNSW life stages and life-stage outcomes, and adds two new outcomes focused on egg and larval growth. Table 1 and figure 1 are updated accordingly. The updated version of figure 1 also appears in the cover illustration of this update.

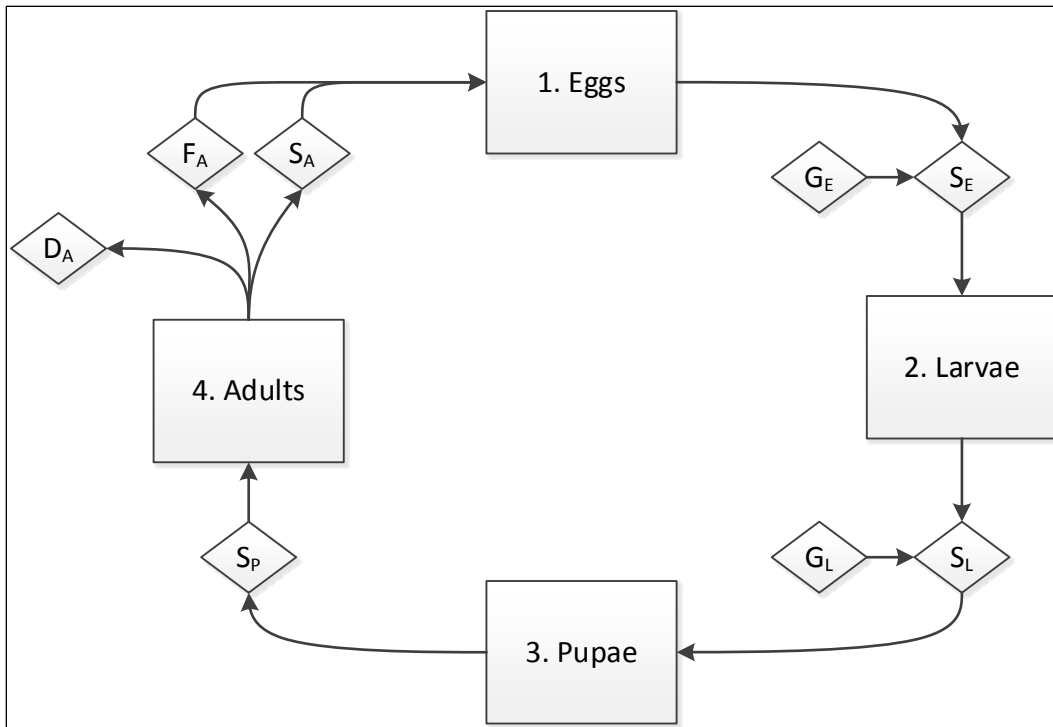
Specifically, the present update standardizes the names of MNSW life stages by switching to the plural noun form for each name, for consistency with the other LCR MSCP conceptual ecological model updates. The names of the original life-stage outcomes are standardized as follows: (1) “Survivorship Rate” changes to “Survival” for all four life stages, (2) “Adult Reproductive Output” changes to “Adult Fertility,” and (3) “Adult Dispersal Rate” changes to “Adult Dispersal.” This update drops the word “rate” from the names of life-stage outcomes because all life-stage outcomes are rate variables by definition.

Table 1.—Revision of original table 1 – MNSW life stages and life-stage outcomes in the LCR ecosystem

Life stage	Life-stage outcome(s)
1. Eggs	<ul style="list-style-type: none"><li>• Egg survival</li><li>• Egg growth</li></ul>
2. Larvae	<ul style="list-style-type: none"><li>• Larval survival</li><li>• Larval growth</li></ul>
3. Pupae	<ul style="list-style-type: none"><li>• Pupal survival</li></ul>
4. Adults	<ul style="list-style-type: none"><li>• Adult survival to mating</li><li>• Adult fertility</li><li>• Adult dispersal</li></ul>

The present update adds “Egg Growth” and “Larval Growth” as life-stage outcomes for these two life stages, parallel to survival. Egg growth consists of egg maturation to hatching. Larval growth includes increasing body size, morphological development, and transformation (molting) through each instar stage before larval metamorphosis into a pupa. This update adds these two new outcomes to the CEM to capture (1) the ways in which the growth rate can affect the survival rate for these two life stages, (2) the ways in which chemical stress, disease, and thermal stress potentially can affect egg growth, and (3) the ways in which competition, chemical stress, disease, mechanical stress, thermal stress, and foraging success can affect larval growth.

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**Figure 1.—Revision of original figure 1 – Proposed MNSW life history model.** Squares indicate the life stage, and diamonds indicate life-stage outcomes. Life-stage outcomes are rates, as follows:  $S_E$  = survival of eggs;  $G_E$  = growth of eggs;  $S_L$  = survival of larvae (caterpillars);  $G_L$  = growth of larvae (caterpillars);  $S_P$  = survival of pupae;  $S_A$  = survival of adults to mating;  $F_A$  = fertility of adults at mating; and  $D_A$  = dispersal of adults from their natal sites.

This update also adds to the discussions of the individual life stages, as follows:

## Eggs

The original CEM (Braun 2015) noted that published studies of MNSW eggs and hatching (e.g., Wiesenborn 2012a) do not discuss the possible effects of extreme temperatures on MNSW egg hatching or rates of hatching success. This update notes that exposure to temperature extremes is a known cause of altered egg development in butterflies (Woestmann and Saastamoinen 2016) but remains unstudied in MNSW specifically.

## Larvae

The original CEM (Braun 2015) incorrectly noted uncertainty about how larval activity varies with time of day. Pratt and Wiesenborn (2011) indicate that at least older larvae “hide during most of the day” inside their leaf shelters.

The original CEM (Braun 2015) did not note that MNSW larvae pass through two instar stages, generally termed the early and late or first and second instars (LCR MSCP 2016; MacNeill 1970; Nelson et al. 2015; Pratt et al. 2015; Wiesenborn 2012a). MNSW larvae live in shelters on the quailbush leaves on which they feed (Greeney and Jones 2003; LCR MSCP 2009, 2013; Pratt and Wiesenborn 2011; Greeney et al. 2012; Wiesenborn 2012a). Smaller larvae make shelters consisting of cut leaf sections, while larger, older larvae make shelters of one or more entire leaves folded over and held together with silk threads (Nelson et al. 2015; Pratt and Wiesenborn 2011). The literature on MNSW otherwise does not identify any ecological differences between the two instars that might warrant treating them as separate life stages in the CEM.

The original CEM (Braun 2015) also did not note that MNSW larvae may aestivate (undergo extended diapause) during summer periods of seasonal drought. Nelson et al. (2015) note, “Variation in precipitation as it affects host plant growth influences diapause in butterflies... Extended diapause that occurs in late instar larvae or pupae is often observed in Lepidoptera that live in areas of seasonal drought ... Diapause is often broken after rains that provide moisture and encourage host plant growth ... Some skippers found in areas with low and unpredictable rainfall aestivate for months as late instar larvae, with the adult flight season highly responsive to rainfall episodes... MacNeill’s sootywing may have similar strategies and responses to rainfall events along the LCR.” Aestivating butterfly larvae exhibit no growth, with greatly slowed metabolism and breathing (Scott 1986). If seasonal drought is the main trigger of larval aestivation, MNSW larvae will experience such seasonal drought through their sensing of leaf moisture as noted by Nelson et al. (2015). However, quailbush in irrigated or subirrigated areas in the LCR ecosystem may not experience seasonal deficits in quailbush leaf moisture.

Dietary restrictions during the larval stage potentially can affect butterfly adults and subsequent generations as discussed in chapter 3 (see “Foraging”). Such dietary restrictions in natural settings can arise as a result of drought or other factors that impair the availability or nutritional quality of their host plants. The restriction can affect not only larval growth rates and duration but also adult morphology, foraging and mating behavior, fecundity, and physiology and development in subsequent generations (Awmack and Leather 2002; Boggs 2003; Boggs and Niitepõld 2014; Gibbs et al. 2012, 2018; Johnson et al. 2014; Rosa and Saastamoinen 2017; Saastamoinen et al. 2013; Vande Velde et al. 2013; Woestmann and Saastamoinen 2016). These relationships have been observed across numerous butterfly species but have not been studied specifically in MNSW or any closely related species.

The update to chapter 3 concerning foraging notes that some older literature suggests MNSW larvae prefer the “young foliage” of quailbush (NatureServe 2018). If this is a correct observation, it could occur as a consequence of one or two processes: adult females could oviposit directly on young leaves or larvae

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could move to them as they forage and grow. However, none of the literature from the LCR ecosystem reviewed for this CEM reports such a preference among MNSW females or larvae for younger leaves. Rather, the literature records a preference among adult females for ovipositing on leaves with other characteristics, such as lushness, that could themselves vary with leaf age (see chapter 3, “Ovipositing”). Hill and Ronning (2018, joint personal communication) also note that MNSW larvae are easier to see on younger quailbush leaves: younger quailbush leaves are darker than older leaves, and the light coloration of the larvae stands out better against this darker background. On the other hand, larval feeding can cause extensive damage to individual leaves (Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 2012a), which should enhance field detection regardless of leaf coloration. Also, as discussed under “Quailbush Shrub Condition” in the original CEM (Braun 2015), MNSW female adults strongly prefer to lay their eggs on quailbush with high leaf moisture content and a very low proportion of dry leaves. If these latter properties vary with shrub and/or leaf maturity, this would result in the concentration of larvae on younger leaves, at least initially after MNSW egg hatching. It thus remains unclear, whether MNSW larvae have a preference for younger leaves, and whether they consequently move specifically to younger leaves whenever they abandon one leaf shelter to reestablish themselves elsewhere on their natal shrub.

## **Pupae**

The original CEM (Braun 2015) noted a statement by Pratt and Wiesenborn (2011) that pupation takes place in a leaf shelter. Photographs of MNSW pupae in the literature and online consistently show the pupae inside leaf shelters, into which the photographers have cut to expose the pupae for recording. However, the original CEM also noted an earlier statement by Pratt and Wiesenborn (2009), based on observations of MNSW reared by the senior author (Pratt) in laboratory cages, that larvae “... likely crawl down to the base of the plant to pupate in leaf litter.” No new observations directly address this potential contradiction. However, it should be noted that MNSW larvae construct their leaf shelters by some combination of bending and cutting quailbush leaves as described above. Such effort likely would not be possible with dry, brittle leaves, either on the shrub or in the litter below. Consequently, the present update questions whether MNSW ever pupate in leaf litter. If a MNSW pupa were to be found in leaf litter, it seems more likely it arrived there by falling when its leaf shelter became dry and dropped from its branch. The question of whether MNSW pupae can occur in quailbush leaf litter has management implications, as irrigation actions and fire management can affect the litter.



## Adults

As noted above (see “Larvae”), dietary restriction during the larval stage can affect adult butterfly morphology, foraging and mating behavior, fecundity, and physiology and development. These effects may appear not only in the adults that emerge from the stressed larvae but also in subsequent generations. However, as also noted above, investigators have studied these relationships in numerous butterfly species but not specifically in MNSW or any closely related species.

A few recent observations add to the otherwise still scant information on adult dispersal. MNSW recolonized Cibola Island, part of the Cibola National Wildlife Refuge, following a fire that burned most of the island in 2011 (J. Hill and C. Ronning 2018, joint personal communication), repeating a pattern seen after the 2006 fire on the island (Nelson et al. 2017, 2018; Wiesenborn 2017). MNSW occupy nearby sites in the Cibola Valley Conservation Area, other parts of the Cibola National Wildlife Refuge, and Hart Mine Marsh (Nelson et al. 2015, 2017, 2018; Wiesenborn 2017). Similarly, MNSW also now occur in the Pretty Water Conservation Area, across the river to the west of Cibola Island (J. Hill and C. Ronning 2018, joint personal communication), where they were not previously known to occur. Published reports do not indicate MNSW distributions along this section of the LCR with sufficient detail to determine the possible sources from which MNSW could have recolonized Cibola Island following the 2011 fire or colonized the Pretty Water Conservation Area, or the dispersal distances involved. However, spatial data on file with the LCR MSCP potentially could be used to pursue this question (J. Hill and C. Ronning, 2018, joint personal communication).

Hill and Ronning (2018, joint personal communication) also note more generally that quailbush can volunteer along the edges of disturbed habitat, such as along irrigation ditches. These investigators suggest that the resulting linear or curvilinear distributions of quailbush could provide corridors for MNSW dispersal.

MNSW dispersal may be triggered by significant rainfall events. Pratt and Wiesenborn (2009) propose that summer rainfalls may increase quailbush plant water content and stimulate late season MNSW adult flights. Nelson et al. (2015) note, “... the highest number of sootywing detections occurred in August of 2014 in conjunction with heavy precipitation just prior to sampling. Variation in precipitation as it affects host plant growth influences diapause in butterflies... Extended diapause that occurs in late instar larvae or pupae is often observed in Lepidoptera that live in areas of seasonal drought... Diapause is often broken after rains that provide moisture and encourage host plant growth... Some skippers found in areas with low and unpredictable rainfall aestivate for months as late instar larvae, with the adult flight season highly responsive to rainfall episodes... MacNeill’s sootywings may have similar strategies and responses to

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rainfall events along the LCR. These erratic population changes may require repeated sampling at some locations.” Davenport (2018) similarly suggests that the timing of MNSW flights, as with other desert butterflies, depends “on good rainfall and the timing of those rains.” MNSW dispersal necessarily must occur during one of their seasonal flights. Consequently, MNSW dispersal may be triggered by significant rainfall events. No other literature on MNSW addresses factors that may trigger its dispersal.

## Updates to Chapter 3 – Critical Biological Activities and Processes

This update eliminates two original critical biological processes, “Contamination and Infection” and “Physiological Stress,” and replaces them with—and integrates their original information into—the biologically more specific categories of “Chemical Stress,” “Disease,” “Mechanical Stress,” and “Thermal Stress.” This update also adds “Competition” as a critical process for consistency with the LCR MSCP conceptual ecological models for other species. The following paragraphs describe the details of these changes.

### CHEMICAL STRESS

This new critical process incorporates portions of the component, “Contamination and Infection,” included in the original CEM (Braun 2015), to better differentiate types of stress. The structure of the resulting updated model parallels that applied to LCR MSCP conceptual ecological models for other terrestrial species. The critical process is defined as follows:

MNSW, as with all butterflies, are vulnerable to stress and mortality in every life stage due to exposure to harmful chemical contaminants (Nelson and Andersen 1999) or to natural chemicals at extreme concentrations. For example, selenium is a naturally occurring element that can reach potentially biologically harmful concentrations in LCR surface waters—a matter of long-standing concern (LCR MSCP 2016, 2018; Ohmart et al. 1988). Like many plants, quailbush can bioaccumulate selenium (Meyer 2005). Selenium can harm herbivorous insects that consume contaminated plant matter (Awmack and Leather 2002), although no studies have evaluated the possibility for MNSW in particular. MNSW potentially can be exposed to extreme concentrations of naturally occurring chemicals through ingestion from quailbush leaves (MNSW larvae) or nectar sources (MNSW adults). Quailbush leaves may also have high concentrations of common salt ions,  $\text{Na}^+$  and  $\text{Cl}^-$ . The literature does not indicate whether or how leaf salt content may affect MNSW larvae or ovipositing (see below).

Anthropogenic chemicals may disrupt insect health and/or impair growth, development, or reproduction. MNSW in all life stages potentially can encounter harmful anthropogenic chemicals through direct contact – MNSW larvae through ingestion from quailbush leaves and MNSW adults through their nectar sources. The LCR MSCP Habitat Conservation Plan (Bureau of Reclamation [Reclamation] 2004) recognizes that the LCR MSCP may apply anthropogenic chemicals in its conservation areas to help establish or maintain desired vegetation for covered bird species. The Habitat Conservation Plan states that LCR MSCP efforts will include “...methods that minimize the need for

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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 may use pesticides to control unwanted ant species in conservation areas and may use herbicides to control non-native plants (LCR MSCP 2014, 2018). However, the literature 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 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 to produce crops such as alfalfa (*Medicago sativa*) and cotton. Chemical use on such adjacent fields potentially could result in contamination of MNSW habitat either through wind transport of sprayed chemicals or through chemical leaching into shallow groundwater. At least some butterfly species are known to be highly sensitive to agricultural neonicotinoid pesticides (Pecenka and Lundgren 2015).

Davenport (2018) identifies several butterfly species in southern California for which pesticide exposure may be a critical threat, although this list does not include MNSW. The LCR MSCP recognizes agricultural pesticide contamination as a potential risk factor for other species under its management (LCR MSCP 2016), although not presently for MNSW.

Reclamation biologists (R. Wydoski and S.M. Nelson 2015, personal communication) observed one instance where Fremont cottonwoods (*Populus fremontii*) 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, or bactericides) by aerial spraying, and drift from aerially sprayed pesticides potentially could reach MNSW habitat sites. Cotton farmers may also aerially apply some herbicides to promote faster leaf drop prior to harvesting.

The literature records no instances in which contaminants from adjacent farmlands are known or suspected to have affected any MNSW habitat sites. Nevertheless, the CEM must at least recognize the possibility of such interactions. Chapter 4 also discusses the types of chemical contaminants to which MNSW might be exposed to along the Lower Colorado River Valley and the potential consequences of chemical contamination on quailbush shrub condition.

## COMPETITION

This new critical process is added so that the CEM better addresses this important process, which the original CEM (Braun 2015) addressed under the habitat element, “Competitors,” and their effects on critical processes such as “Foraging.” The structure of the resulting updated model parallels that applied to LCR MSCP conceptual ecological models for other terrestrial species. The critical process is defined as follows:

MNSW larvae and adults must compete with other species for food and habitat, as must all animal species. Competition can limit the ability of MNSW to access habitat space or acquire water or nutrients, or can have bioenergetic costs by forcing MNSW to travel farther to acquire needed resources.

Chapters 4 and 6 discuss the range of competitors facing MNSW in these two life stages. Specifically, as discussed below (see chapter 4, “Arthropod Assemblage”), MNSW must compete with other arthropods that feed on quailbush leaves, including the larvae of other butterfly species. Similarly (see chapter 4, “Vertebrate Assemblage”), MNSW must compete with mammals that may browse on quailbush leaves. MNSW also must compete with numerous Lepidoptera species that may use MNSW nectar source plants as their larval hosts and/or as nectar sources.

The literature does not report on competition among MNSW for host plant space or nectar sources, although such competition is theoretically possible. However, the present critical biological process in the CEM refers specifically to competition of MNSW with other species. The CEM addresses competition among MNSW larvae and among MNSW adults for food by recognizing the relationship between survival and foraging as a bi-directional relationship for both life stages.

MNSW males compete with each other for mates. However, again, the present critical biological process in the CEM refers specifically to competition of MNSW with other species. The critical biological process, “Mating,” addresses competition among MNSW males for mates.

Every animal species evolves strategies that permit its persistence despite such competition, including specific behaviors that allow it to avoid or defend against it. Avoidance behaviors may include an evolved preference for resources other than those preferred by other species in the system (resource partitioning) or an evolved ability to switch among alternative resources as needed. MNSW do not exhibit any flexibility in their selection of larval host plant species. However, their exclusive use of quailbush may itself be an evolved adaptation, as few other

species tolerate—let alone prefer—the highly saline quailbush leaves (see “Foraging,” this chapter). In turn, MNSW adults show wide flexibility in their foraging for nectar among multiple potential sources.

Quailbush also compete for space, water, and nutrients with other plants. However, the present critical biological process in the CEM refers specifically to competition affecting MNSW itself. The habitat elements, “Quailbush Patch Distribution,” “Quailbush Patch Size and Structure,” and “Quailbush Shrub Condition” address competition affecting quailbush itself.

## **DISEASE**

This new critical process incorporates portions of the component, “Contamination and Infection,” included in the original CEM (Braun 2015) to better differentiate types of stress. The structure of the resulting updated model parallels that applied to LCR MSCP conceptual ecological models for other terrestrial species. The critical process is defined as follows:

MNSW in all life stages are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction.

Parasitic infections are a common challenge for butterflies in general, to which all species have evolved arrays of defenses (Altizer and de Roode 2010; Greeney and Jones 2003; Greeney et al. 2012; Gross 1993; Rosa et al. 2017). 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 particular parasitoid species that use MNSW as their host. The literature reviewed for this CEM also does not provide information on the types or frequencies of evidence for parasitism among MNSW of any life stage. Wiesenborn (2010a) specifically notes a need for studies of parasitism on MNSW to support habitat conservation.

Similarly, the literature does not report on the incidence of viral, bacterial, or fungal infections among MNSW, and it does not report on diseases that potentially can affect MNSW or environmental factors that might affect their incidence. Greeney et al. (2012) suggest that aggregating behavior potentially can make it easier for infections to spread among butterfly larvae. Rosa et al. (2017), on the other hand, suggest that gregarious butterfly larval species may have heightened immune responses to compensate. MNSW larvae appear mostly to disperse to individual leaves after hatching (LCR MSCP 2016; MacNeill 1970; Pratt and Wiesenborn 2011), reducing this risk factor more directly.

## FORAGING

The name of this critical activity, formerly “Feeding/Watering” (Braun 2015), has been standardized in this update to “Foraging.” Further, the definition of this critical process has been updated as follows concerning larval and adult feeding:

As discussed in chapter 2, some older literature suggests MNSW larvae prefer the “young foliage” of quailbush (see literature cited in NatureServe 2018). If MNSW females do not oviposit directly on young leaves, MNSW larvae presumably must move to them as they forage and grow. Studies along the LCR do not report a preference for younger leaves but do record preferences for ovipositing on leaves with characteristics that could vary with leaf age (see “Ovipositing,” this chapter). Hill and Ronning (2018, joint personal communication) also note that MNSW larvae are easier to see on younger quailbush leaves because younger quailbush leaves are darker than older leaves, and the light coloration of the larvae stands out better against this darker background. This raises the possibility that the perception of larval preference for younger leaves may be a consequence of visibility. However, larval feeding can cause extensive damage to individual leaves, which enhances field detection (Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 2012a). Also, as discussed under “Quailbush Shrub Condition” in the original CEM (Braun 2015), MNSW female adults strongly prefer to lay their eggs on quailbush with high leaf moisture content and a very low proportion of dry leaves. If these properties vary with shrub and/or leaf maturity, this would result in the concentration of larvae on younger leaves, at least initially after MNSW egg hatching.

Recent studies note that plants in the family Chenopodiaceae, which includes quailbush, produce distinctive epidermal salt glands, known as salt bladders, in which they concentrate  $\text{Na}^+$  and  $\text{Cl}^-$  ions (LoPresti 2014, 2016; Nikalje et al. 2017; Shabala et al. 2014). These structures are thought to contribute to the ability of the plant to tolerate and even thrive in soils with high concentrations of salt. The high concentrations of salt in these bladders may make them and the leaves of which they are parts unpalatable to herbivores. Further (LoPresti 2014), the bladders eventually burst, covering the leaf in a highly salty residue that may also reduce palatability.

LoPresti (2014) and Shabala et al. (2014) document the presence of salt bladders on the undersides of quailbush leaves, as well as on the leaf undersides of several other members of the same genus. The bladders may cover the entire undersides of the leaves, including young leaves (LoPresti 2014; Shabala et al. 2014). Panta et al. (2016) observed that the  $\text{Na}^+$  and  $\text{Cl}^-$  ion content of quailbush leaves varies with the salinity of the soil moisture available. At the same time, Meyer (2005) and Panta et al. (2016) indicate that quailbush tolerates a wide range of soil salinities without experiencing stress (see chapter 4, “Soil Salinity”). However,

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the literature on MNSW does not contain information on quailbush salt bladders or quailbush leaf salt content, or information on how MNSW larvae respond to either.

This update also revises the list of species that MNSW adults may use as nectar sources. Specifically, table 2 incorporates information from Nelson et al. (2015) that MNSW may use quailbush itself as a nectar source. The authors report observing two MNSW adults foraging for nectar on quailbush in August 2014, at study plots along the Colorado River between Laughlin, Nevada, and the Cibola National Wildlife Refuge south of Blythe, California. The authors note that, to their knowledge, quailbush had not previously been reported as a nectar plant for MNSW. As noted in the original MNSW conceptual ecological model (Braun 2015), Wiesenborn (1997) proposes that adult MNSW do not feed on quailbush flowers because they are wind pollinated and therefore do not produce nectar. However, while members of the genus *Atriplex* generally are wind pollinated, Meyer (2005) found no specific evidence of this for quailbush.

Table 2.—Revision of original 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>Melilotus officinalis</i> , yellow sweetclover	O	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> Origin Key: N = native and O = non-native.

Table 2 also incorporates information from Hill and Ronning (2018, joint personal communication) that MNSW have been observed feeding on non-native yellow sweetclover (*Melilotus officinalis*). (The information concerning table 3 in the original CEM otherwise does not require updating.)



Finally, numerous studies have used butterflies as models (Burton and Metcalfe 2014) for exploring general hypotheses concerning the effects of juvenile (including larval) dietary restriction on adults and subsequent generations. Among butterflies in natural settings, such restriction can arise as a result of drought or other factors that impair the availability or nutritional quality of their host plants. Studies across a wide range of butterfly species suggest that impaired diets among larvae not only affect larval growth rates and duration but can also affect adult morphology, foraging and mating behavior, fecundity, and physiology and development in subsequent generations (Awmack and Leather 2002; Boggs 2003; Boggs and Niitepõld 2014; Gibbs et al. 2012, 2018; Johnson et al. 2014; Rosa and Saastamoinen 2017; Saastamoinen et al. 2013; Vande Velde et al. 2013; Woestmann and Saastamoinen 2016). These relationships have been observed across numerous butterfly species (see review by Woestmann and Saastamoinen 2016), but have not been studied in any species closely related to MNSW, let alone specifically in MNSW. Whether or to what extent MNSW can experience such immediate and transgenerational effects of larval foraging impairment are matters for future investigation.

## **MATING**

The definition of this critical process has been updated as follows:

The potential effects of butterfly larval dietary restriction, discussed above (see “Foraging,” this chapter) include effects on wing morphology and mating behavior among the adults that emerge from larvae that faced dietary limitations (Awmack and Leather 2002; Boggs 2003; Boggs and Niitepõld 2014; Woestmann and Saastamoinen 2016). Whether or to what extent MNSW can experience such immediate and transgenerational effects of larval foraging impairment are matters for future investigation.

## **MECHANICAL STRESS**

This new critical process incorporates portions of the component, “Physiological Stress,” included in the original CEM (Braun 2015) to better differentiate types of stress. The structure of the resulting updated model parallels that applied to LCR MSCP conceptual ecological models for other terrestrial species. The critical process is defined as follows:

MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to intense precipitation or harmful winds, and capture and handling for study. Unavoidable or inescapable mechanical stresses may kill or weaken individual MNSW, or disrupt growth, development, or

reproduction. As noted below in this chapter (see “Resting/Hiding”), MNSW larvae and adults display a range of behaviors for avoiding or escaping potentially stressful conditions. Additionally, as noted below in this chapter (see “Ovipositing,” this chapter), adult females preparing to lay their eggs appear to select locations within quailbush shrubs and select shrubs within vegetation patches that provide shelter from a range of potentially stressful conditions (see “Thermal Stress,” this chapter).

Specifically, MNSW adults hide within quailbush canopies when windspeeds 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 windspeeds “...up to five (18–24 miles per hour, [29–38 kilometers per hour] on the Beaufort scale.” However, the surveys of MNSW habitat reported by Nelson et al. (2014, 2015) only “... occurred at windspeeds that were less than or equal to a light breeze (< 7 miles per hour [11.3 kilometers per hour], 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.

However, MNSW larvae or adults may be unable to avoid or escape some mechanically stressful conditions or, in the case of ovipositing females, unable to anticipate the occurrence of such conditions. Examples of potential conditions that could result in unavoidable or inescapable mechanical 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 (Calvert 2008; Conway et al. 2010; Elmore et al. 2003; MacNally et al. 2004; Meyer 2005; NatureServe 2018; Nelson and Andersen 1999; Nelson et al. 2014; Pratt and Wiesenborn 2011; Stromberg et al. 2007; Wiesenborn 2012b), as discussed in chapter 4 of the original CEM report (Braun 2015).

## **OVIPOSITING**

The definition of this critical process is updated as follows:

The potential effects of butterfly larval dietary restriction (see “Foraging,” this chapter) include effects on feeding behavior and leaf selection for ovipositing among the adult females that emerge from larvae that faced dietary limitations (Awmack and Leather 2002; Boggs 2003; Boggs and Niitepõld 2014; Gibbs et al. 2018; Johnson et al. 2014; Rosa and Saastamoinen 2017; Woestmann and Saastamoinen 2016). Whether or to what extent MNSW can experience such immediate and transgenerational effects of larval foraging impairment on ovipositing are matters for future investigation.

## PREDATION

The definition of this critical process is updated as follows:

MNSW in every life stage are vulnerable to predation by both arthropods and vertebrates, as are all butterflies (Greeney et al. 2012; Hoskins 2015; Scott 1986). The new habitat elements for the CEM, “Arthropod Assemblage” and “Vertebrate Assemblage,” capture information on the range of predators that MNSW may face and the habitat settings in which they may face them.

Every animal species evolves strategies that permit its persistence despite predation, including behaviors that help the species avoid or defend against it. For example, Thaler et al. (2012) describe compensatory aggregation behavior among butterfly larvae in the presence of an arthropod predator, although MNSW are not known to exhibit such behavior. On the other hand, MNSW larval behavior, such as their use of leaf shelters, likely indicates adaptation to both predation and parasitism (Greeney et al. 2012; see “Resting/Hiding,” this chapter). Wiesenborn and Pratt (2008) also suggest that “... More rapid development increases larval survival by reducing exposure to predators and parasites.” MNSW adults, in turn, hide within quailbush vegetation, remain very still when basking (rest with wings open) or perching, and exhibit erratic flight behavior (a hallmark of skippers), all of which may help the adults avoid avian predators (see “Resting/Hiding,” this chapter). Beyond these few reports, however, the literature contains little information concerning predation on MNSW or ways in which MNSW may have adapted to predation pressure. Wiesenborn (2010a) identifies the absence of information on predation as a significant gap in knowledge of MNSW ecology.

## RESTING/HIDING

The name of this critical activity, formerly “Hiding/Resting” (Braun 2015), has been standardized to “Resting/Hiding” for consistency with other CEMs and to clarify its meaning. The definition also has been updated in several ways, including incorporating information included in the original CEM in the definition of “Physiological Stress.” The revised definition is as follows:

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.

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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 (Nelson et al. 2015; Pratt and Wiesenborn 2011). This is a common shelter type among Hesperidae, the family of MNSW (Greeney and Jones 2003). The larvae remain in their shelter when not feeding, which may be most of the day (Nelson et al. 2015; Pratt and Wiesenborn 2011). Pratt and Wiesenborn (2011) indicate that at least older larvae “hide during most of the day” inside their leaf shelters. The literature reviewed for this CEM otherwise does not report on whether larval activity varies with time of day.

Hesperidae 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 (Greeney and Jones 2003; Greeney et al. 2012; Nelson et al. 2015; Pratt and Wiesenborn 2011). 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 rest at night. This may be because some nectar species close at night (Wiesenborn and Pratt 2010) and MNSW rely on visual cues to locate their preferred nectar sources (Wiesenborn 2010b). However, MNSW adults also spend most of their daylight hours within the quailbush canopy, particularly during the hottest hours of the day and for longer periods on days with extremely high temperatures, 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). LCR MSCP investigators have proposed avoiding trying to monitor MNSW adult activity between 13:30 and 16:00 because MNSW may be less active during these hours and, therefore, less readily observed (Nelson et al. 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 (J. Hill and C. Ronning 2018, joint personal communication; Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 1997). Theoretically, adult MNSW within the 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,” this chapter).

Additionally (see “Ovipositing,” this chapter), 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. In addition (see “Mechanical Stress,” this chapter), MNSW hide within quailbush canopies when windspeeds rise to potentially challenging levels.

MNSW adults do sometimes rest on the outer leaves of the quailbush canopy, specifically when basking. Ronning (2018, personal communication) notes that basking generally occurs on the sides of the shrubs at heights of 0.5–1.0 meter, and reports observing an adult MNSW in April 2018 basking on bare soil alongside an irrigation ditch. However, Ronning (2018, personal communication) also cautions, “...not all surface-type preferences for MNSW basking are known. It is also unknown if a lack or limited amount of their preferred basking surfaces affects presence or [vegetation] uses.” MNSW bask in the open, in sunlight, presumably to raise their body temperature when the air is cool; 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; this behavior increases as daytime temperatures increase up to some threshold but then decreases above this threshold (Pratt and Wiesenborn 2009).

Ronning (2018, personal communication) further notes that MNSW are “very still” when basking or perching, and this stillness makes it more difficult to detect them during field investigations. “They can be hard to detect due to their small size and the mottled shade of the shrubs even when perched on the outside of a quailbush until they start flying again. That stillness would have made it hard to detect [the] one I saw basking on the ground if I hadn’t been following it at the time.” As a corollary, one may hypothesize that the stillness could also affect the detectability of basking or perching MNSW by predators scanning quailbush canopies.

## THERMAL STRESS

This new critical process incorporates portions of the component, “Physiological Stress,” included in the original CEM (Braun 2015) to better differentiate types of stress. The structure of the resulting updated model parallels that applied to LCR MSCP conceptual ecological models for other terrestrial species. The critical process is defined as follows:

MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Unavoidable or inescapable thermal stresses may kill or weaken individual MNSW, or disrupt growth, development, or reproduction. However, as discussed in detail in chapter 2 in the original CEM (Braun 2015) and above (see “Resting/Hiding,” this chapter), MNSW larvae and adults display a range of behaviors for avoiding or escaping potentially thermally stressful conditions.

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These behaviors include the larval use of leaf shelters and adult use of shade, greatly reduced adult activity during the hottest hours of the day, and resting with wings closed. In contrast to their behavior during hotter days and hours, MNSW adults conversely may bask in sunlight with their wings open presumably to raise their body and wing temperatures for flight.

## Updates to Chapter 4 – Habitat Elements

This update eliminates two original habitat elements, “Competitors” and “Predators,” and replaces them with the more biologically specific “Arthropod Assemblage” and “Vertebrate Assemblage.” It also adds “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” so that the CEM better addresses vegetation structure around quailbush patches. As a consequence of these change in vegetation habitat elements, this update also eliminates the original habitat element, “Nectar Sources.” It incorporates the relevant ecological information from this original habitat element into the two new vegetation elements. Finally, this update renames one original habitat element for purposes of standardization. The following paragraphs describe these changes.

### ARTHROPOD ASSEMBLAGE

This is a new habitat element in the CEM, included so that the CEM better distinguishes different broad categories of competitors and predators. The habitat element is defined as follows:

**Full name:** The taxonomic composition, size range, spatial and temporal distributions, and abundance of the arthropod assemblage in and around quailbush patches used and not used by MNSW. The arthropods of concern may include spiders, ants, beetles, butterflies and moths, and other insects that compete with or prey on MNSW, or otherwise contribute to ecological dynamics in these patches.

MNSW potentially face competition from arthropods that feed on quailbush or on the plants from which MNSW adults obtain nectar. Two other species of butterflies present in the LCR ecosystem also use quailbush as a larval host: the saltbush sootywing,<sup>1</sup> (*Hesperopsis alpheus*) and the western pygmy blue (*Brephidium exilis*) (Robinson et al. 2018; Scott 1986). Nelson et al. (2015) and Pratt and Wiesenborn (2011) have specifically recorded the presence of both species in vegetation patches occupied by MNSW, and Nelson et al. (2015) observed one individual of *B. exilis* “laying eggs on quail bush seed heads.” Quailbush is a secondary host for saltbush sootywing, which primarily uses the fourwing saltbush (*Atriplex canescens*) rather than quailbush (Robinson et al. 2018; Scott 1986). Western pygmy blue use a large number of species as host plants in the region, including not only fourwing saltbush and quailbush but also

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<sup>1</sup> Scott (1986) classifies MNSW as a subspecies of *H. alpheus*; however, *H. graciellae* is genetically close to, but nevertheless distinct from, *H. alpheus* (Pratt et al. 2015), and standard taxonomies do not recognize the subspecies classification (Integrated Taxonomic Information System 2018).

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other members of the family Chenopodiaceae (Robinson et al. 2018; Scott 1986). Neither saltbush sootywing nor western pygmy blue therefore likely strongly competes with MNSW for host habitat resources.

Pratt and Wiesenborn (2011) and Nelson et al. (2015) also provide lists of other butterfly species that occur in vegetation patches occupied by MNSW. These other species include marine blue (*Leptotes marina*), Ceraunus blue (*Hemiargus ceraunus*), Reakirt's blue (*Echinargus [Hemiargus] isola*), checkered white (*Pontia protodice*), orange sulfur (*Colias eurytheme*), dainty sulfur (*Nathalis iole*), common checkered-skipper (*Pyrgus communis*), Eufala skipper (*Lerodea eufala*), and fiery skipper (*Hylephila phyleus*). Nelson et al. (2015) do not indicate whether any of these species use quailbush in particular. Neither Scott (1986) nor Robinson et al. (2018) report these other species using quailbush as a host plant.

Additionally, Nelson et al. (2015) identify other non-Lepidopteran arthropods on quailbush in vegetation patches occupied by MNSW. These other arthropods may compete with MNSW for nutrition from quailbush and include “*Ensign coccids* (?*Orthezia*), aphids (Aphidoidea), galls (various insects), grasshoppers (Orthoptera), egg-laying damage caused by cicadas (*Diceroprocta apache*), and the moth *Trichocosmia inornata*. *Trichocosmia inornata* was identified by DNA analysis from a caterpillar found feeding on quail bush. *Ensign coccids* were especially common at the Needles plot where they appeared to impact quail bush health to some degree.”

The literature reviewed for this CEM did not include observations concerning which other species of Lepidoptera in the LCR ecosystem may use the same nectar sources as MNSW. The arthropod assemblage along Las Vegas Wash, Nevada, an area that historically supported MNSW, but presently apparently does not (Andersen and Nelson 2013; Eckberg 2011, 2012; Nelson 2009; Nelson and Wydoski 2013; Scott 1986), currently includes several taxa that may feed on floral nectar (Eckberg 2011). These include some mosquitoes, wasps, bees, ants, and net-winged insects such as Chrysopidae: lacewings. Ants may also feed on extra-floral nectar (Aranda-Rickert et al. 2014), although this has not been studied for the plant and ant species along the LCR ecosystem. Otherwise, the range of potential arthropods that may compete with MNSW for nectar is not known.

Data are available, on the other hand, on species of Lepidoptera present in the LCR ecosystem that use MNSW nectar source plants as their larval *host* plants (see updated list of MNSW nectar sources in chapter 3, “Foraging,”). Feeding by the larvae of these other species of Lepidoptera potentially can harm the host plant, thereby reducing the quantity or quality of nectar they produce. The other species of Lepidoptera hosted by MNSW nectar sources therefore may compete with MNSW for nutrients. Table 3 lists every species of Lepidoptera that occurs in the LCR ecosystem and is known or suspected to use an MNSW nectar source plant as a host for its larvae, based USDA and USFHA (2017) and Robinson et al.



## Updates to Chapter 4 – Habitat Elements

Table 3.—New table for this update – Lepidoptera in LCR ecosystem known or suspected to use MNSW nectar sources as larval hosts (USDA and USFHA 2017; Robinson et al. 2018)

Nectar source species	Lepidoptera larval species hosted ( <b>Highlight</b> indicates larval species known or suspected to damage the flowers and/or fruiting bodies.)
<i>Bebbia juncea</i> , sweetbush	<i>Calephelis wrighti</i>
<i>Coriandrum sativum</i> , Chinese parsley	<i>Papilio machaon</i>
<i>Heliotropium curassavicum</i> , salt heliotrope	(No hosted Lepidoptera species listed)
<i>Malvella leprosa</i> , alkali mallow	<i>Heliopetes lavianus</i> , <i>Pyrgus albescens</i> , <i>Pyrgus scriptura</i> , <i>Strymon columella</i> , <i>Strymon columella istapa</i> , <b><i>Strymon melinus</i></b> , <i>Tischeria omissa</i> , <i>Vanessa annabella</i> , <i>Zenodoxus canescens</i> , <i>Zenodoxus canescens sidae</i>
<i>Medicago sativa</i> , alfalfa	<i>Actebia fennica</i> , <i>Anticarsia gemmatalis</i> , <i>Aphelia alleniana</i> , <i>Arachnis picta</i> , <i>Archips argyrospila</i> , <i>Archips rosana</i> , <i>Autographa californica</i> , <i>Colias alexandra</i> , <i>Colias eurytheme</i> , <i>Colias philodice</i> , <i>Discestra trifolii</i> , <i>Echinargus (Hemiargus) isola</i> , <i>Elasmopalpus lignosellus</i> , <i>Erynnis funeralis</i> , <i>Euxoa ochrogaster</i> , <b><i>Glaucopsyche lygdamus</i></b> , <i>Helicoverpa zea</i> , <i>Heliothis phloxiphaga</i> , <b><i>Heliothis virescens</i></b> , <b><i>Hemiargus ceraunus</i></b> , <i>Hydraecia immanis</i> , <i>Hypena scabra</i> , <i>Hyphantria cunea</i> , <i>Lacanobia atlantica</i> , <i>Lacinipolia lorea</i> , <i>Lacinipolia lustralis</i> , <i>Lacinipolia renigera</i> , <i>Lacinipolia stricta</i> , <i>Lacinipolia vicina</i> , <b><i>Leptotes marina</i></b> , <i>Loxostege sticticalis</i> , <b><i>Lycaeides melissa</i></b> , <i>Mamestra configurata</i> , <i>Megalographa biloba</i> , <i>Melanchra adjuncta</i> , <i>Melanchra picta</i> , <i>Nymphalis californica</i> , <i>Papaipema nebris</i> , <i>Peridroma saucia</i> , <i>Platynota nigrocervina</i> , <i>Platynota stultana</i> , <i>Protorthodes incincta</i> , <i>Pseudoplusia includens</i> , <i>Sparganothis sulfureana</i> , <i>Sparganothis unifasciana</i> , <i>Spilosoma virginica</i> , <i>Spodoptera eridania</i> , <i>Spodoptera exigua</i> , <i>Spodoptera frugiperda</i> , <i>Spodoptera ornithogalli</i> , <i>Spodoptera praefica</i> , <b><i>Strymon melinus</i></b> , <i>Thorybes pylades</i> , <i>Trichoplusia ni</i> , <i>Vanessa cardui</i> , <b><i>Xenotemna pallorana</i></b> , <i>Xestia c-nigrum</i> , <i>Xylena nupera</i> , <i>Zerene cesonia</i> , <i>Zerene eurydice</i>
<i>Melilotus officinalis</i> , yellow sweetclover	<i>Actebia fennica</i> , <i>Autographa californica</i> , <i>Automeris io</i> , <i>Biston betularia</i> , <b><i>Celastrina argiolus</i></b> , <i>Colias eurytheme</i> , <i>Colias occidentalis</i> , <i>Colias philodice</i> , <b><i>Echinargus (Hemiargus) isola</i></b> , <i>Estigmene acrea</i> , <i>Euxoa costata</i> , <i>Euxoa declarata</i> , <b><i>Everes comyntas</i></b> , <b><i>Glaucopsyche lygdamus</i></b> , <i>Helicoverpa zea</i> , <i>Hypena scabra</i> , <i>Leptarctia californiae</i> , <i>Mamestra configurata</i> , <i>Omiodes simialis</i> , <i>Papaipema nebris</i> , <i>Parectopa occulta</i> , <i>Peridroma saucia</i> , <b><i>Plebejus acmon</i></b> , <i>Spodoptera praefica</i> , <b><i>Strymon melinus</i></b>
<i>Pluchea sericea</i> , arrowweed	<i>Schinia intrabilis</i>
<i>Portulaca oleacea</i> , common purslane	(No hosted Lepidoptera species listed)
<i>Prosopis glandulosa</i> , honey mesquite	<i>Anacamptodes fragilaria</i> , <i>Apodemia palmerii</i> , <i>Atlides halesus</i> , <i>Bulia deducta</i> , <i>Carmenta phoradendri</i> , <i>Carmenta prosopis</i> , <b><i>Cydia membroza</i></b> , <b><i>Echinargus (Hemiargus) isola</i></b> , <b><i>Ectomyelois ceratoniae</i></b> , <i>Friseria cockerelli</i> , <b><i>Hemiargus ceraunus</i></b> , <i>Hemileuca junco</i> , <i>Hemileuca tricolor</i> , <b><i>Ithome concolorella</i></b> , <b><i>Leptotes marina</i></b> , <i>Melipotis indomita</i> , <b><i>Ministrymon leda</i></b> , <i>Periploca orichalcella</i> , <i>Pococera euphemella</i> , <i>Rachiplusia ou</i> , <i>Semiothisa cyda</i> , <i>Synchlora frondaria</i> , <i>Synchlora frondaria</i> , <i>Syssphinx helligbrodti</i> , <i>Urbanus proteus</i>
<i>Prosopis pubescens</i> , screwbean mesquite	<i>Apodemia palmerii</i> , <b><i>Hemiargus ceraunus</i></b> , <i>Hemileuca junco</i>
<i>Sesuvium verrucosum</i> , verrucose seapurslane	<b><i>Brephidium exilis</i></b> , <i>Heliodines prenticei</i>
<i>Tamarix ramosissima</i> , saltcedar	(No hosted Lepidoptera species listed)

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(2018). Trathnigg and Phillips (2015) found that, among riparian restoration sites in the LCR ecosystem, butterfly species richness correlated with flowering plant richness and abundance, vegetation species diversity, and herbaceous plant cover.

Table 3 also highlights those Lepidoptera species specifically known or suspected to damage the flowers and/or fruiting bodies of each host plant species. This subset of Lepidoptera species may compete more strongly with MNSW adults for nutrients because they directly damage the flowers from which MNSW obtains its nectar. The highlighted species include four recorded by Pratt and Wiesenborn (2011) and Nelson et al. (2015) at sites occupied by MNSW: Western pygmy blue, marine blue, ceraunus blue, and Reakirt's blue. Given their known presence at sites occupied by MNSW and their ability to damage the flowering bodies of MNSW nectar sources, these four species may compete more substantially with MNSW for the nutrient resources of MNSW nectar source plants than may other species highlighted in table 3. As noted above, western pygmy blue larvae may also compete with MNSW larvae for quailbush nutrients; however, no systematic data were identified for this update on actual larval use of MNSW nectar sources by any of these Lepidoptera species.

None of the literature reviewed to prepare the present CEM provides information on arthropod predation specifically on MNSW. The general literature on butterflies notes that their arthropod predators may include spiders, ants, wasps, dragonflies, robber flies, crickets, and mantises (Hoskins 2015; Scott 1986; Tiitsaar et al. 2013). Richard Wydoski (2015, personal communication) suggests native praying mantises (insects of the Order, Mantodea) and spiders as possible types of invertebrate predators on MNSW in the Lower Colorado River Valley. Mantises would hunt in the foliage; spiders would be expected to hunt and trap both within the foliage and within the leaf litter beneath quailbush shrubs; and ants would be expected to hunt larvae in the foliage. Field reports routinely mention the presence of these types of arthropods in MNSW habitat (e.g., Nelson and Andersen 1999; Nelson and Wydoski 2013), and recent field studies of MNSW habitat maintain records of these observations. Quailbush patches attract numerous species of insectivorous birds (Meyer 2005), indicating that the patches likely attract abundant arthropods as well. As noted in chapter 3 (see "Predation"), the absence of information on predation is a significant gap in knowledge of MNSW ecology.

## **CHEMICAL CONTAMINANTS**

The current review did not find any new literature on this topic with which to update the definition in the original CEM (Braun 2015). Hill and Ronning (2018, joint personal communication) report that the LCR MSCP does not have access to data on chemical use on the agricultural fields adjacent to MNSW sites along the LCR ecosystem.

## FIRE REGIME

The definition and discussion of this habitat element is updated as follows:

One study has found that the sensitivity of honey mesquite (*Prosopis glandulosa*) to fire varies with the seasonal timing and intensity of fire (Ansley et al. 2015). However, the study took place in a different ecoregion, Chihuahuan, with a different seasonal climate, in an area with a grass ground cover that significantly affected fire properties, and focused on seedling mortality. The results may or may not apply to honey mesquite in the LCR ecosystem.

## HERBACEOUS VEGETATION ASSEMBLAGE

This is a new habitat element in the CEM, included so that the CEM better addresses important properties of the herbaceous vegetation in and around quailbush patches. The updated terminology also parallels that used in LCR MSCP conceptual ecological models for other terrestrial species. The habitat element is defined as follows:

***Full name:* The taxonomic composition and density, and spatial and temporal variation in these properties, of the herbaceous vegetation assemblage in and around quailbush patches successfully and unsuccessfully occupied by MNSW.** As indicated in the “Definitions” for this CEM (following the Acronyms and Abbreviations list), herbaceous vegetation consists of vascular species that are 0.5 meter or less in height. Shrubs, consisting of woody plants between 0.5 and 2.0 meters in height, are considered part of the woody vegetation assemblage (see below, this chapter). MNSW use several herbaceous plant species as nectar sources. Herbaceous vegetation in the LCR ecosystem provides habitat for arthropods, ground-dwelling birds, reptiles and adult amphibians, and mammals, some of which may prey on or compete with MNSW (see “Arthropod Assemblage” and “Vertebrate Assemblage,” this chapter). Herbaceous vegetation potentially can compete with shrubs such as quailbush for space.

MNSW do not occupy all quailbush patches within their geographic range along the LCR ecosystem. Surveys along the LCR as of 2008 from the Bill Williams River to the international border found MNSW at only 59% of quailbush stands (LCR MSCP 2009) despite the widespread presence of the butterfly across this geographic range. These survey results indicate that “The presence of host plants alone does not assure the presence of the butterfly.” MNSW may select among quailbush patches based in part on quailbush condition (see “Quailbush Patch Size and Structure” and “Quailbush Shrub Condition” in Braun ([2015] chapter 3).

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Accidents of history presumably also play a role in shaping the local distribution of MNSW (e.g., in relation to vegetation disturbance). For example, Ronning (2018, personal communication) has observed changes in herbaceous vegetation and MNSW occupancy at Hunters Hole. This is the most southerly of the LCR MSCP conservation areas, located on the historic Colorado River floodplain approximately 3 miles north of the U.S./Mexico Southerly International Boundary. Ronning (2018) reports, "In Oct[ober] 2014, there was a fire at Hunters Hole. ... The fire was centered in Cell 3 and was approximately 5.58 acres in size. The fire was low in intensity and moved along slowly through the grassy areas, causing some minor scorching of honey mesquite, willows, and cottonwoods. The fire was completely extinguished by Bureau of Land Management fire suppression efforts and flood irrigation conducted by Reclamation. Most of the trees that were scorched survived. Much of the grass and herbaceous vegetation was consumed. In spring 2015, there was flowering [of] herbaceous vegetation and grass throughout the cell. We detected MNSW there in spring 2015. There was also a pulse flow for Minute 319 that brought water down the dry LCR riverbed on the west side of the site in [the] spring of 2014. I'm not sure if this helped with MNSW dispersal to the site. There is quailbush in and along the riverbed and MNSW may be present there. We can't check as its right on the [U.S./Mexico] border line. [The MNSW] may have been attracted to the quailbush as it matured in Hunters Hole (the site was planted in 2013), or by the herbaceous flowering in 2015 post-fire, or followed the water/quailbush response to river flowing." The literature reviewed for this CEM does not otherwise indicate whether, how, or why herbaceous plant cover may vary between quailbush patches occupied versus not occupied by MNSW.

Quailbush is a common plant along the LCR ecosystem and historically occurred in clumps with arrowweed (*Pluchea sericea*) in close association (Grinnell 1914; Nelson et al. 2014; Reynolds et al. 2014). The current vegetation of the LCR ecosystem has been altered from its historic character (Ohmart et al. 1988) as a result of river regulation, direct soil and vegetation disturbance by human activity, livestock grazing, land conversion to farming with associated irrigation and drainage, fire control, and introductions of non-native plants and animals. Within this altered landscape, quailbush can occur in a wide range of local environmental settings, including active floodplain and wetland margins, desert scrub, and isolated alkaline sinks (Meyer 2005).

For example, Reynolds et al. (2014), found quailbush on two of seven landforms surveyed along the Bill Williams River below Alamo Dam in April 2010. Reynolds et al. (2014) found quailbush on high terraces and ephemeral wash surfaces, but not on the currently active floodplain, abandoned floodplain surfaces, low terraces, or uplands. The quailbush on the high terraces and ephemeral wash surfaces occurred in association with arrowweed, honey mesquite, and saltcedar but not in association with any MNSW herbaceous nectar sources. (MNSW do occur along the Bill Williams River Valley, at least in the Bill Williams River National Wildlife Refuge [LCR MSCP 2009; Nelson and

Andersen 1999]). However, Reynolds et al. (2014) provide no information on the butterflies or other arthropods encountered at their survey locations.

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% quailbush followed by the woody native, honey mesquite; herbaceous native, alkali mallow; native woody shrub, desertbroom; woody non-native, saltcedar; and native herbaceous arrowweed. The MNSW herbaceous nectar sources, salt heliotrope (*Heliotropium curassavicum*) and verrucose seapurslane, comprised an average 3% of the cover.<sup>2</sup>

Nelson et al. (2015) also collected data on relative cover by plant species among MNSW nectar sources in sampling plots at multiple sites occupied by MNSW. The authors report the findings in the form of an overall floral index, a summary indicator of nectar source richness and abundance, including both herbaceous and woody species. The authors found that the index did not vary significantly among surveyed plots or from month to month. “Saltcedar (*Tamarix* spp.), alfalfa (*Medicago sativa*), mesquite, and arrowweed (*Pluchea sericea*) appeared to be the most common sources of nectar. Alkali heliotrope and sea purslane, considered important nectar plants for sootywings, were rarely encountered. Overall, the floral index suggested low diversity and amounts of flowers and nectar in the environment for most months ... with few plant species recorded as ... abundant at plots. Higher index values were observed in May ... but this month did not differ significantly from other months.”

Nelson et al. (2015) also note that the floral index used for this study did not include quailbush in its species list. The index was designed prior to the observations of MNSW foraging for nectar on quailbush in August of the study year, 2014 (see chapter 3, “Foraging”). However, including quailbush in the species list for the index potentially would only further reduce the variation in index values among the sampled plots: The study focused on sites known to be occupied by MNSW, which necessarily contain quailbush, although individual sampling plots at a site need not always have contained quailbush shrubs.

Soil salinity potentially could be a factor in determining which quailbush patches MNSW prefer. As noted in the original CEM (Braun 2015), quailbush tolerate highly saline soils (Meyer 2005). Quailbush also can grow in soils with low salinity and may colonize such settings following soil disturbance (Meyer 2005). However, its tolerance of high soil salinity gives it a competitive advantage over many other desert riparian plants in such settings (Meyer 2005) other than saltcedar (Nagler et al. 2011; Pratt and Wiesenborn 2011). Therefore, it may be

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<sup>2</sup> As noted above, Reynolds et al. (2014) recorded no herbaceous nectar sources in association with quailbush at the sites they surveyed along the Bill Williams River Valley; however, MNSW may not have occurred at the sites surveyed by Reynolds et al. (2014): The surveyors did not collect such data.

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notable that, except for sweetbush, all of the native herbaceous nectar sources used by MNSW also tolerate or prefer soils with high salinity (USDA 2018).

The proximity of nectar sources also may affect MNSW preferences among quailbush patches and/or the ability of quailbush patches to support MNSW. MNSW adults seek out and feed on “nearby” nectar sources (Pratt and Wiesenborn 2011; Wiesenborn and Pratt 2008), but the literature provides few data on absolute foraging distances. Wiesenborn (1997) reports frequently observing individuals flying across distances of approximately 4 meters between quailbush shrubs and mesquite, presumably to feed on extrafloral nectar. At the same time, Wiesenborn (1997) also reports MNSW “...feeding at flowers of *B. juncea* ... ~ 0.15 miles (0.25 kilometer) from the study site and the only insect-pollinated plants in flower in the vicinity.” MNSW also seek out salt heliotrope plants, and individual flowers on these plants, based on the appearance of the flower petals in visible and ultraviolet light (Wiesenborn 2010b, 2011). Additionally, MNSW adult females seek out flowers with higher nectar sugar content apparently in a quest for nutrition (Nelson et al. 2015; Wiesenborn 2010a, 2011; Wiesenborn and Pratt 2010).

It therefore seems likely that MNSW adult foraging distances and directions—particularly among females—will vary with the spatial distribution of nectar sources, but with limits on their overall foraging radius. The spatial distribution of nectar sources varies seasonally. Pratt and Wiesenborn (2009) found that selection of species for feeding varied over the annual cycle, presumably in synchrony with flowering. Feeding on salt heliotrope dominated beginning in April but ended late in June; feeding on arrowweed peaked in late June–early July; and feeding on saltcedar peaked in late August (Pratt and Wiesenborn 2009). Quailbush patches with greater abundances of nearby nectar sources over a wider seasonal span therefore will likely have a greater ability to support MNSW.

MNSW adult females also seek out quailbush with a leaf-nitrogen content > 3.2% (LCR MSCP 2009; Wiesenborn and Pratt 2008), and amino acids (which contain nitrogen) in nectar may be an important nutrient at least for adult female MNSW, as for adult female butterflies in general (Boggs 2003; Nelson et al. 2015; Pratt and Wiesenborn 2009; Rosa et al. 2017; Vande Velde et al. 2013; Wiesenborn and Pratt 2010). These relationships suggest a possibility that MNSW may prefer quailbush patches growing on soils with sufficient nitrogen to support attractive concentrations of nitrogen in the quailbush leaves and amino acids in nectars. Quailbush and mesquite—including its seedlings—fix nitrogen through their roots (Meyer 2005; Steinberg 2001; USDA 2018). Hypothetically, if litter from these species affects nitrogen in the surrounding

soils, herbaceous nectar sources growing in and around healthy stands of quailbush and mesquite may produce nectar with higher concentrations of amino acids. However, the literature reviewed for this CEM does not address these possible relationships.

Finally, the composition and density of the herbaceous vegetation assemblage in and around quailbush patches likely affects the composition of the arthropod assemblage in and around these patches. Nelson and Andersen (1999) found that revegetated sites in the LCR ecosystem lacked the herbaceous vegetation richness of sites in the Bill Williams River National Wildlife Refuge with natural vegetation and that butterfly diversity was correspondingly lower at the revegetated sites. Tepedino et al. (2008) found that the addition of non-native nectar sources to riparian sites in southern Utah increased the attractiveness of the sites to nectar-feeding arthropods without reducing the abundance of native nectar sources. Nelson (2009) found that herbaceous assemblage richness was important in structuring butterfly assemblage composition along Las Vegas Wash, and as noted above (see “Arthropod Assemblage,” this chapter), Trathnigg and Phillips (2015) found that, among riparian restoration sites in the LCR ecosystem, butterfly species richness correlated with flowering plant richness and abundance, vegetation species diversity, and herbaceous plant cover. The attractiveness of quailbush patches to insectivorous birds and mammals presumably would vary with the abundance of arthropods; however, this potential set of ecological relationships has not been studied systematically in the ecoregion.

## **INFECTIOUS AGENTS**

No change.

## **INUNDATION REGIME**

The discussion of this habitat element is updated to note that inundation of the litter beneath quailbush shrubs, through irrigation, can result in wet quailbush litter (J. Hill and C. Ronning 2018, joint personal communication). Wet litter may provide different habitat values for arthropods, birds, and mammals that may use the litter, in addition to affecting any MNSW pupae that may be present, and wet litter will be less likely to burn during prescribed fires or wildfires.

## **MONITORING, CAPTURE, HANDLING**

The name of this habitat element, formerly “Scientific Study” (Braun 2015), has been standardized in this update to “Monitoring, Capture, Handling.” Further, the definition of this critical process has been expanded as follows:

The monitoring of environmental DNA (eDNA) has proven effective, in combination with colored paper strip attractants, to monitor adult MNSW during their searches for nectar (J. Hill and C. Ronning 2018, joint personal communication). However, it is not clear whether the eDNA methods can distinguish between deoxyribonucleic acid (DNA) from MNSW and DNA from genetically closely related species such as saltbush sootywing. The LCR MSCP also has modified its field monitoring methods for MNSW (J. Hill and C. Ronning 2018, joint personal communication). Under the modified field protocols, the field crews do not return later in the year to resurvey any monitoring transects in which a crew has already detected the presence of MNSW in the same year. This modification reduces the incidence of potentially harmful contact with MNSW and increases the number of locations that crews can survey in the field season. The resulting data allow the LCR MSCP to map the total area of occupancy, and the number, sizes, and spatial distribution of occupied patches, but do not allow the estimation of overall or within-patch abundance. As noted above (see “Resting/Hiding”), LCR MSCP investigators also have proposed avoiding monitoring MNSW adult activity between 13:30 and 16:00, the hottest hours of the day, because MNSW may be less active during these hours and therefore less readily observed (Nelson et al. 2015).

## **QUAILBUSH LITTER CONDITION**

The discussion of this habitat element is updated, as is the discussion of the inundation regime (see above, this chapter), to note that inundation of quailbush patches through irrigation can result in wet quailbush litter (J. Hill and C. Ronning 2018, joint personal communication). Wet litter may provide different habitat values for arthropods, birds, and mammals that may use the litter, in addition to affecting any MNSW pupae that may be present, and wet litter will be less likely to burn during prescribed fires or wildfires. Conversely, dry litter beneath individual quailbush shrubs conceivably could help fuel fires in quailbush patches (Meyer 2005).

## **QUAILBUSH PATCH DISTRIBUTION**

No change.



## QUAILBUSH PATCH SIZE AND STRUCTURE

No change.

## QUAILBUSH SHRUB CONDITION

No change.

## SOIL MOISTURE

The discussion of this habitat element is updated to note that quailbush can grow in areas with depths to the water table exceeding 5 feet (Meyer 2005), such as elevated floodplain terraces (Nelson and Andersen 1999; Reynolds et al. 2014). Meyer (2005) interprets these facts to indicate that quailbush in areas with deep water tables "... are likely to survive on surface sources of soil moisture and be less vigorous than specimens that occur in areas with a shallow water table." However, the presence of quailbush in areas with deep water tables alternatively may indicate that quailbush can extend their roots downward to maintain contact with soil moisture under drying conditions once they have successfully rooted in soils with sufficient moisture at the ground surface (J. Hill and C. Ronning 2018, joint personal communication). Such a capability, if verified, could have implications for quailbush patch management. Quailbush can spread along the margins of irrigation ditches in the LCR ecosystem (J. Hill and C. Ronning 2018, joint personal communication), indicating that they readily colonize moist soils when present. Quailbush can tolerate the salinities found in irrigation return water very well (Panta et al. 2016).

Ronning (2018) also notes the following concerning the effects of soil moisture on quailbush, herbaceous vegetation, and woody vegetation in areas where soil moisture previously was sustained by irrigation but where irrigation has been curtailed: "We have reduced irrigation in a number of established honey mesquite patches in order to use the water in areas with the cottonwood-willow land cover. Grasses have been reduced or died off and in some of the phases the quailbush appears to be showing stress (have more bare branches) and there is little to no quailbush recruitment except in the areas where soil moisture is available (along irrigation ditches that had water in them to irrigate other areas and edges of roads)."

## SOIL NITROGEN

No change.

## SOIL SALINITY

The discussion of this habitat element is updated to take note of information added to the CEM under the headings of “Foraging” and “Herbaceous Vegetation Assemblage” (see chapter 3 and the present chapter, respectively).

Specifically, quailbush appear to cope with high soil salinity in part by excreting excess salt, incorporated during root water uptake, into salt bladders on the undersides of their leaves (see chapter 3, “Foraging”). Quailbush in fact can also grow across a wider range of settings but have an adaptive advantage over many other plants in its ability to thrive on saline soils. In turn, MNSW may be narrowly adapted to using quailbush in areas of saline soils. As noted above (see “Herbaceous Vegetation,” this chapter), all of the native herbaceous nectar sources used by MNSW, except sweetbush, also tolerate or prefer soils with high salinity, as does saltcedar, the most heavily used non-native nectar source for MNSW (USDA 2018).

## VERTEBRATE ASSEMBLAGE

This is a new habitat element in the CEM, included so that the CEM better distinguishes different broad categories of competitors and predators. The definition incorporates substantial material from the sections on competitors and predators (see chapter 4 in the original CEM report [Braun 2015]). The habitat element is defined as follows:

***Full name:* The taxonomic composition, size range, spatial and temporal distributions, and abundance of the vertebrate assemblage in and around quailbush patches successfully and unsuccessfully occupied by MNSW.** The assemblage includes birds, mammals, and reptiles and amphibians, some of which may prey on MNSW, prey on arthropods or other vertebrates that could otherwise prey on or compete with MNSW, consume quailbush leaves, or consume the leaves, flowers, seeds, or nectar of MNSW nectar source species. Seed-eating vertebrates also potentially could affect the overall composition of the herbaceous and woody vegetation assemblages. The taxonomic composition, size range, spatial and temporal distributions, and abundance of the vertebrate assemblage in and around quailbush patches will vary depending on the suitability of the larger environment containing these patches, including the availability of suitable cover or perches. For purposes of this CEM, the relevant properties of this

larger environment are captured under the headings of two other habitat elements, “Herbaceous Vegetation Assemblage,” and “Woody Vegetation Assemblage.”

Butterflies, in general, face risks of predation by insectivorous birds overhead and by insectivorous, ground-foraging birds from below. MNSW pupae and larvae on low-lying branches are 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 Lower Colorado River Valley from 1976 to 1980, 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% of their diet during one or more seasons.

Table 4.—Revision of original table 5 – Proportion of Lepidoptera in diets of insectivorous birds by season, Lower Colorado River Valley, 1976–80 (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

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 use 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. Foraging activity by ground-feeding birds in the litter beneath quailbush shrubs presumably also could disturb the litter. The possible effects of such disturbance on MNSW pupae are not known. The literature reviewed for the CEM provided no information on nectarivorous birds (e.g., hummingbirds) that may feed on MNSW nectar sources.

A variety of mammals also can occur in or make use of quailbush patches (Anderson 2012). Meyer (2005) notes that mule deer (*Odocoileus hemionus*), pronghorn (*Antilocapra americana*), rabbits, rodents, goats, and other livestock browse quailbush leaves, and deer mice (*Peromyscus maniculatus*) eat the seeds, although not as a first choice. Some or all of these herbivores, and others, presumably may browse on the herbaceous and woody vegetation surrounding quailbush patches.

The literature reviewed for the CEM provides no information on vertebrate predation on MNSW. Potential vertebrate predators on butterflies, in general, include lizards, frogs, toads, mice, and other rodents (Scott 1986), numerous species of which can occur in the LCR ecosystem (Anderson 2012; Ohmart et al. 1988). Other possible vertebrate insectivores in the LCR ecosystem include skunks (e.g., striped skunks [*Mephitis mephitis*], raccoons [*Procyon lotor*], and ringtails [*Bassaricus astutus*]) (Ohmart et al. 1988).

## **WOODY VEGETATION ASSEMBLAGE**

This is a new habitat element in the CEM, included so that the CEM better addresses important properties of the woody vegetation in and around quailbush patches. The updated terminology also parallels that used in LCR MSCP conceptual ecological models for other terrestrial species. The habitat element is defined as follows:

**Full name:** The taxonomic composition, density, vertical structure, and spatial and temporal distributions of the woody vegetation assemblage in and around quailbush patches successfully and unsuccessfully occupied by MNSW. Woody vegetation occurs in and around quailbush patches as both canopy and shrub vegetation (see “Definitions” following the Acronyms and Abbreviations list). Woody canopy vegetation, when present, can provide shade over individual quailbush shrubs. Woody vegetation can provide habitat for

arthropods, cover for ground-dwelling birds, perches for arboreal birds, and cover for mammals, reptiles, and amphibians that may prey on or compete with MNSW (see “Arthropod Assemblage” and “Vertebrate Assemblage,” this chapter). MNSW use two tree species and one woody shrub species as nectar sources. In turn, the woody non-native saltcedar can compete with quailbush, native woody vegetation, and herbaceous vegetation for space and water, and its removal can result in further ecological change.

As discussed above (see “Herbaceous Vegetation Assemblage,” this chapter), quailbush are common plants along the LCR ecosystem; they historically occurred in clumps with both herbaceous and woody arrowweed in close association (Grinnell 1914; Nelson et al. 2014; Reynolds et al. 2014). The current vegetation of the LCR ecosystem has been altered from its historic character (Ohmart et al. 1988) as a result of river regulation, direct soil and vegetation disturbance by human activity, livestock grazing, fire control, land conversion to farming with associated irrigation and drainage, and introductions of non-native plants and animals. Within this altered landscape, quailbush can occur in a wide range of local environmental settings, including active floodplain and wetland margins, desert scrub, and isolated alkaline sinks, with varying surrounding woody vegetation (Meyer 2005).

Reynolds et al. (2014), found quailbush on two of seven landforms surveyed along the Bill Williams River below Alamo Dam in April 2010, as discussed above (see “Herbaceous Vegetation Assemblage,” this chapter): on high terraces and ephemeral wash surfaces but not on the currently active floodplain, abandoned floodplain surfaces, low terraces, or uplands. The quailbush on both the high terraces and ephemeral wash surfaces occurred in association with both herbaceous and woody arrowweed, honey mesquite, and saltcedar but not in association with any MNSW herbaceous nectar sources. Reynolds et al. (2014) provide no information on the butterflies or other arthropods encountered at their survey locations, although MNSW do occur in at least the Lower Bill Williams River Valley (LCR MSCP 2009; Nelson and Andersen 1999).

Transects surveyed by Pratt and Wiesenborn (2009) at one site occupied by MNSW (see “Herbaceous Vegetation Assemblage, above) contained 37–76% quailbush by area of coverage, followed by honey mesquite (woody); alkali mallow (*Malvella leprosa*) (herbaceous); desert broom (aka greasewood), *B. sarothroides* (woody); saltcedar (woody); and arrowweed (herbaceous when small, woody when mature). As discussed above (see “Herbaceous Vegetation Assemblage,” this chapter), Nelson et al. (2015) also collected data on vegetative cover—specifically, nectar sources—in sampling plots at multiple sites occupied by MNSW. The authors report the findings in the form of an overall floral index, a summary indicator of nectar source richness and abundance, including both herbaceous and woody species. The index did not vary significantly among surveyed plots or from month to month, with saltcedar, alfalfa, mesquite, and arrowweed the most common nectar sources in all plots.

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MNSW do not occupy all quailbush patches within their geographic range along the LCR ecosystem (see “Herbaceous Vegetation Assemblage,” this chapter). Surveys along the LCR as of 2008 from the Bill Williams River to the international border found MNSW at only 59% of quailbush stands (LCR MSCP 2009) despite the widespread presence of the butterfly across this geographic range. MNSW may select among quailbush patches based, in part, on quailbush condition (see chapter 3, “Quailbush Patch Size and Structure” and “Quailbush Shrub Condition” in Braun [2015]).

Accidents of history presumably also play a role in shaping the local distribution of MNSW (e.g., in relation to vegetation disturbance). For example, as noted above for herbaceous vegetation, Ronning (2018, personal communication) observed changes in vegetation and MNSW occupancy at Hunters Hole following both fire and hydrologic disturbance. Ronning (2018) reports, “In Oct[ober] 2014, there was a fire at Hunters Hole... The fire was centered in Cell 3 and was approximately 5.58 acres in size. The fire was low in intensity and moved along slowly through the grassy areas, causing some minor scorching of mesquite, willows, and cottonwoods. The fire was completely extinguished by Bureau of Land Management fire suppression efforts and flood irrigation conducted by Reclamation. Most of the trees that were scorched survived. Much of the grass and herbaceous vegetation was consumed. In spring 2015, there was flowering [of] herbaceous vegetation and grass throughout the cell. We detected MNSW there in spring 2015. There was also a pulse flow for Minute 319 that brought water down the dry LCR riverbed on the west side of the site in [the] spring of 2014. I’m not sure if this helped with MNSW dispersal to the site. There is quailbush in and along the riverbed and MNSW may be present there. We can’t check as its right on the [U.S./Mexico] border line. [The MNSW] may have been attracted to the quailbush as it matured in Hunters Hole (the site was planted in 2013), or by the herbaceous flowering in 2015 post-fire, or followed the water/quailbush response to river flowing.”

In addition, MNSW may prefer quailbush shrubs that are shaded by woody canopy vegetation presumably because the canopy helps them avoid thermal stress (J. Hill and C. Ronning 2018, joint personal communication; Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 1997). On the other hand, the presence of too many large stature honey mesquite trees within and around quailbush patches could reduce quailbush shrub condition and the availability of herbaceous nectar sources in those patches, inhibiting MNSW use of the affected patches (Nelson et al. 2014).

The data reported by Nelson et al. (2015), Pratt and Wiesenborn (2009), and Reynolds et al. (2014) indicate that quailbush do not typically occur in association with two native riparian tree species in the LCR ecosystem – Fremont cottonwood and Goodding’s willow (*Salix gooddingii*). However, J. Hill and C. Ronning (2018, joint personal communication) report that quailbush occupied by MNSW can occur adjacent to these two woody species at LCR MSCP restoration sites,

where these trees can provide shade. On the other hand, Ronning (2018) cautions that the occurrence of MNSW on quailbush adjacent to these two woody species could also be a consequence of the fact that the LCR MSCP irrigates cottonwood-willow patches, resulting in elevated soil moisture for other plants at these locations, including quailbush.

Soil salinity potentially affects which quailbush patches MNSW prefer, as discussed above (see “Herbaceous Vegetation Assemblage”). As noted in the original CEM (Braun 2015), quailbush tolerate highly saline soils (Meyer 2005). Quailbush also can grow in soils with low salinity and may colonize such settings following soil disturbance (Meyer 2005). However, its tolerance of soils with high salinity gives it a competitive advantage in such soils over many other desert riparian plants (Meyer 2005) other than saltcedar (Nagler et al. 2011; Pratt and Wiesenborn 2011). It therefore may be notable that all of the woody nectar sources used by MNSW, both the two native mesquite species (honey and screwbean), the native arrowweed, and the non-native saltcedar, also tolerate or prefer soils with high salinity (USDA 2018).

The proximity of woody nectar sources also may affect MNSW preferences among quailbush patches and/or the ability of quailbush patches to support MNSW. As discussed above (see “Herbaceous Vegetation Assemblage,” this chapter) and in the original CEM (Braun 2015), MNSW adults seek out and feed on “nearby” nectar sources (Pratt and Wiesenborn 2011; Wiesenborn and Pratt 2008). However, the literature provides few data on absolute foraging distances. Wiesenborn (1997) provides the greatest amount of information on foraging distances and reports observing individuals easily and repetitively flying across a distance of approximately 4 meters between quailbush and honey mesquite canopy edges. MNSW appear to have been exploiting the extrafloral nectaries on the mesquite, which Wiesenborn (1997) observed to be active at the time of the study, when the mesquite trees were not in flower.

The spatial distribution of nectar sources in fact varies seasonally. Pratt and Wiesenborn (2009) found that MNSW selection of species for feeding varied over the annual cycle. This seasonal variation in feeding preference presumably synchronized with flowering activity and, based on the observations of Wiesenborn (1997), the availability of extrafloral nectar as well. Wiesenborn (1997) found that feeding on salt heliotrope dominated beginning in April but ended late in June; feeding on arrowweed peaked in late June–early July; and feeding on saltcedar peaked in late August (Pratt and Wiesenborn 2009). Honey mesquite flowering occurs between April and August depending on seasonal conditions (Calflora 2018; Steinberg 2001). The observations of MNSW flights between quailbush and honey mesquite by Wiesenborn (1997) coincided with the presence of mesquite extrafloral nectar production in September. Quailbush patches with greater abundances of nectar sources over a wider seasonal span potentially have a greater ability to support MNSW.

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MNSW adult females seek out flowers with higher nectar sugar content, apparently in a quest for nutrition (Nelson et al. 2015; Wiesenborn 2010a, 2011; Wiesenborn and Pratt 2010) (see chapter 3, “Foraging”). As also discussed above concerning herbaceous vegetation, amino acids in nectar may be an important nutrient at least for adult female MNSW as for adult female butterflies in general (Boggs 2003; Nelson et al. 2015; Pratt and Wiesenborn 2009; Rosa et al. 2017; Vande Velde et al. 2013; Wiesenborn and Pratt 2010). These relationships suggest a possibility that MNSW may prefer quailbush patches growing on soils with sufficient nitrogen to support attractive concentrations of nitrogen in the quailbush leaves and amino acids in nectars. Quailbush and mesquite—including its seedlings—fix nitrogen through their roots (Steinberg 2001; Meyer 2005). Hypothetically, if litter from these species affects nitrogen in the surrounding soils, herbaceous nectar sources growing in and around healthy stands of quailbush and mesquite may produce nectar with higher concentrations of amino acids. In addition, because mesquite trees fix nitrogen, their floral and extrafloral nectars may contain suitable, reliable concentrations of amino acids for MNSW. However, the studies reviewed for the present CEM provide no data on the nutritional quality of nectars from the various woody or herbaceous plants that MNSW seek out.

Bacteria associated with honey mesquite root systems also can enhance root uptake of soluble phosphate (Moreno-Ramírez et al. 2015). However, the literature does not indicate whether this relationship affects mesquite floral or extrafloral nectar nutritional quality.

Mesquite extrafloral nectar may attract ants as well as Lepidoptera such as MNSW (Aranda-Rickert et al. 2014). The attraction of ants to extrafloral nectar sources can be a symbiotic relationship, in which the ants attack other arthropods that visit “their” extrafloral source tree, thereby helping protect the tree from arthropods that might otherwise harm it (Aranda-Rickert et al. 2014). Visiting Lepidoptera could then face a risk of attack depending on the type(s) of ant present. However, the literature does not provide any information specifically about ant interactions with mesquite in the LCR ecosystem or MNSW interactions with ants on the mesquite trees they visit for extrafloral nectar.

Saltcedar also may interact with MNSW and quailbush in unique ways that affect MNSW abundance and distribution. As noted above, the non-native saltcedar is a frequent component of the vegetation around quailbush shrubs in the LCR ecosystem. MNSW readily seek out and consume saltcedar floral nectar when it is available (see chapter 3, “Foraging”). In addition, older, taller saltcedar vegetation can provide crucial shade for quailbush and MNSW, as observed at the Pretty Water Conservation Area in recent years (J. Hill and C. Ronning 2018, joint personal communication).

On the other hand, saltcedar is a highly invasive species that competes aggressively with native riparian vegetation throughout the Southwestern United



States, including in the LCR ecosystem (Zouhar 2003). It tolerates saline soils very well (Zouhar 2003). It can out-compete most native woody and herbaceous plants wherever groundwater is sufficiently close to the ground surface to allow the invader to become established, forming large, dense monotypic stands (Merritt and Poff 2010; Meyer 2005; Nagler et al. 2011; Zouhar 2003).

However, quailbush appear to present an exception to this general pattern of saltcedar dominance. Meyer (2005) notes that, in habitats with altered disturbance regimes where saltcedar otherwise would crowd out other native species, “Due to [quailbush] being a ‘vigorous competitor’ on sites where it is already established, these areas may be less likely to follow this pattern.” Once quailbush become established at a location, it can tolerate periods of flooding “for most of a growing season, with some root growth likely during this period” (Meyer 2005), as noted in the original MNSW conceptual ecological model (Braun 2015). On the other hand, Meyer (2005) also states that the strong response of saltcedar after fire could allow it to crowd out previously established quailbush in locations subject to increased fire frequencies.

At the same time, it is not clear how strongly saltcedar and quailbush may compete with each other to colonize newly available habitat where neither is already established. Meyer (2005) documents that quailbush seedlings are much more likely to become established in soils with shallower versus deeper water tables and/or soils that are irrigated or close to an irrigation source, and less likely to become established in dry soils. However, Meyer (2005) does not indicate, for comparison with saltcedar, specifically how quailbush seed germination itself varies with soil moisture.

It is conceivable that large, dense monotypic stands of saltcedar could interfere with MNSW dispersal by occupying potential quailbush habitat over areas too large for MNSW to overfly (Pratt and Wiesenborn 2011; see “Updates to Chapter 2 – MNSW Life Stage Model”). Outside of such monotypic stands, the presence of too many large saltcedar trees merely adjacent to quailbush shrubs potentially may cause excessive shading of the quailbush shrubs and adjacent herbaceous nectar sources, reducing the attractiveness of these locations to MNSW (J. Hill and C. Ronning 2018, joint personal communication). A large body of literature also documents that saltcedar stands harbor different spectra of arthropods, birds, and other vertebrates compared to native riparian communities (Andersen and Nelson 2013; Bateman et al. 2013; Pendleton et al. 2011). The presence of saltcedar in the LCR ecosystem therefore may be either beneficial or detrimental to MNSW depending on the site and whether saltcedar or quailbush colonizes the site first.

Land and water managers throughout the Southwestern United States have fought the spread of saltcedar for decades. Restoration efforts initially involved the killing and, often but not always, removal of individual saltcedar trees and stands using fire, herbicides, and/or mechanical methods. Some restoration projects

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included planned revegetation following removal, while others simply allowed uncontrolled colonization and succession to play out (Andersen and Nelson 2013; Bateman et al. 2013; Bean and Dudley 2018; Nagler et al. 2011; Zouhar 2003). In 2001, intentional release of the non-native northern tamarisk beetle (*Diorhabda carinulata*) in the Upper Colorado River Basin added biocontrol to the toolbox of methods (Bean and Dudley 2018). The beetle has spread widely, including down the Colorado River Valley into the LCR ecosystem, where it currently occurs as far south as the Blythe, California, area (J. Hill and C. Ronning 2018, joint personal communication). Repeated defoliation by the beetle usually causes the canopy to die back within 1 to 4 years and causes plant death within 2 years or more, depending on the site (Bean and Dudley 2018).

The likely effects on MNSW and quailbush from saltcedar defoliation and dieback along the LCR ecosystem in the wake of northern tamarisk beetle attacks are not well understood. These effects may be either beneficial or detrimental to MNSW, depending on the site, as is the case with the presence of saltcedar itself (see above). A loss of saltcedar around individual quailbush patches could result in a loss of a crucial nectar source and crucial shade, or it could open up areas for recolonization by native plants (J. Hill and C. Ronning 2018, joint personal communication). For example, die-offs of formerly monotypic stands of saltcedar could open up habitat for quailbush, mesquite, arrowweed, and herbaceous nectar sources. Studies also suggest that, following the elimination of saltcedar, restoration of habitat quality for native arthropods and birds requires deliberate, controlled revegetation to avoid the emergence of undesirable plant assemblages (Bay and Sher 2008; Bean and Dudley 2018; Eckberg and Rice 2016; González et al. 2017a, 2017b; Kennard et al. 2016; Nagler et al. 2017; Nelson 2009; Nelson and Wydoski 2013; Shafroth et al. 2008; Sogge et al. 2008; Trathnigg and Phillips 2015).

## Updates to Chapter 5 – Controlling Factors

This update standardizes the name of one controlling factor and otherwise leaves the definitions and discussions of the six original controlling factors unchanged.

### **OFFSITE LAND MANAGEMENT AND USE**

No change.

### **ONSITE FIRE MANAGEMENT**

No change.

### **ONSITE VEGETATION MANAGEMENT**

No change.

### **ONSITE VISITATION AND STUDY**

No change.

### **ONSITE WATER MANAGEMENT**

The definition is expanded to note that onsite water management may also include actions to reduce or terminate water applications at a site (e.g., to reallocate water to other sites within the limits of Reclamation water rights).

### **WATER STORAGE-DELIVERY SYSTEM DESIGN AND OPERATIONS**

The name of this controlling factor, formerly “Reach-Scale Water Management” (Braun 2015), has been standardized to “Water Storage-Delivery System Design and Operations” for consistency with other CEMs and to clarify its meaning. The definition and discussion remain the same.

## Updates to Chapter 6 – Conceptual Ecological Model by Life Stage

The following sections identify all changes made to the MNSW conceptual ecological model workbook other than those that involve only updates to names. These latter changes are listed separately in table 5 (see “Summary of Standardization of Terms,” this chapter). The items in each section of this chapter are arranged alphabetically. The abbreviations, CF for controlling factor, HE for habitat element, CAP for critical activity or process, and LSO for life-stage outcome are provided to identify component types where needed. Each item also identifies the life stage(s) to which the item applies.

### NEW LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

- Offsite Land Management and Use Effects on the Herbaceous Vegetation Assemblage (HE): The original CEM (Braun 2015) included a link from this controlling factor to “Competitors,” but only for larvae and adults. This update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” and two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage. The link reason notes that offsite land management and use practices such as farming may allow, actively foster, or actively suppress the presence of particular native and non-native herbaceous plants on the landscape surrounding quailbush patches, including patches occupied or not occupied by MNSW. For example, some farm crops, such as alfalfa, are nectar sources for MNSW, and disturbed areas around field margins may also provide habitat for herbaceous plants that may be native nectar sources. The link is hypothesized to be complex and unidirectional, with proposed high intensity, spatial scale, and temporal scale; low predictability; and medium understanding. *Applies to all life stages.*
- Offsite Land Management and Use Effects on the Vertebrate Assemblage (HE): The original CEM (Braun 2015) included a link from this controlling factor to “Competitors,” which included recognition of potential animal competitors with MNSW, but included this link only for larvae and adults. As noted above, this update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” and two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage.” The link reason notes that

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offsite land management practices such as hunting may directly affect the presence and abundance of particular native and non-native vertebrates on the landscape encompassing quailbush patches, including patches occupied or not occupied by MNSW. The link is hypothesized to be complex and unidirectional, with proposed high intensity, spatial scale, and temporal scale; low predictability; and low understanding. *Applies to all life stages.*

- Offsite Land Management and Use Effects on the Woody Vegetation Assemblage (HE): The original CEM (Braun 2015) included a link from this controlling factor to “Competitors,” but only for larvae and adults. This update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” and two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage.” The link reason notes that offsite land management and use practices such as farming may allow, actively foster, or actively suppress the presence of particular native and non-native woody plants on the landscape surrounding quailbush patches, including patches occupied or not occupied by MNSW. The link is hypothesized to be complex and unidirectional, with proposed high intensity, spatial scale, and temporal scale; low predictability; and medium understanding. *Applies to all life stages.*
- Onsite Vegetation Management effects on the Herbaceous Vegetation Assemblage (HE): The original CEM (Braun 2015) included a link from this controlling factor to “Nectar Sources,” but only for adults. This update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” with the MNSW nectar sources distributed between these two plant categories. The link reason notes that LCR MSCP and partner actions within and immediately surrounding quailbush patches, 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 herbaceous plants in and immediately around these patches whether occupied or not by MNSW. The link is hypothesized to be complex and unidirectional, with proposed medium intensity and spatial scale but unknown temporal scale; low predictability; and medium understanding. The link magnitude reason states that onsite vegetation management has great potential to affect herbaceous vegetation types, abundances, or spatial distributions, but there is no specific program for doing so, and it is not evident how often such actions may be taking place or their effectiveness. *Applies to all life stages.*
- Onsite Vegetation Management effects on the Woody Vegetation Assemblage (HE): The original CEM (Braun 2015) included a link from

this controlling factor to “Nectar Sources,” but only for adults. This update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” with the MNSW nectar sources distributed between these two plant categories. The link reason notes that LCR MSCP and partner actions within and immediately surrounding quailbush patches, 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 woody plants in and immediately around these patches whether occupied or not by MNSW. The link is hypothesized to be complex and unidirectional, with proposed medium intensity and spatial scale but unknown temporal scale; low predictability; and medium understanding. The link magnitude reason states that onsite vegetation management has great potential to affect woody vegetation types, abundances, or spatial distributions, but there is no specific program for doing so, and it is not evident how often such actions may be taking place or their effectiveness. *Applies to all life stages.*

- Onsite Visitation and Study effects on the Arthropod Assemblage (HE): The original CEM (Braun 2015) included links from this controlling factor to “Competitors” and “Predators,” although only for larvae and adults. This update drops the habitat elements, “Competitors” and “Predators,” and, insofar as these original habitat elements concerned animals, replaces them with two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage,” and applies this change to all life stages. The link reason notes that visitors to MNSW habitat sites potentially can accidentally introduce other arthropod species that may “hitchhike” on clothing, soil on boots, vehicles, or equipment. The link is hypothesized to be complex and unidirectional, with proposed unknown intensity, spatial scale, and temporal scale; low predictability; and low understanding. The link magnitude reason states that the relationship is proposed based on a theoretical possibility, but there is no evidence of any introductions of arthropods via visitors or any concern about this evident in LCR MSCP reports. *Applies to all life stages.*
- Water Storage-Delivery System Design and Operations effects on Soil Moisture (HE): This CEM update includes this new link to capture the fact that system-scale water management affects water table elevations across the LCR ecosystem, and these water table elevations, in turn, can affect soil moisture within the rooting zones of quailbush and the herbaceous and woody vegetation with which they share the landscape. The link is hypothesized to be complex and unidirectional, with proposed high intensity but low spatial and temporal scales; high predictability; and high understanding. The link magnitude reason states that the effect should have high intensity but only in limited times and places when

system-scale water management results in a high water table. In turn, the link predictability reason states that the circumstances in which this effect may be active are controlled by Reclamation management of the water delivery system, which is highly predictable because it is constrained by a clear set of rules, and the effects of water management decisions on the water table should also be highly predictable. *Applies to all life stages.*

## **DELETED LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS**

- Effects of Offsite Land Management and Use on Competitors for Larvae and Adults. This update replaces “Competitors” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” insofar as “Competitors” refers to plants. *Applies to larvae and adults.*
- Effects of Offsite Land Management and Use on Nectar Sources for larvae and adults. This update incorporates all MNSW nectar sources into the two new categories of vegetation, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to adults.*
- Effects of Onsite Vegetation Management on Nectar Sources. As noted above, this update replaces “Competitors” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” insofar as “Competitors” refers to plants, and it incorporates all MNSW nectar sources into these two new categories of vegetation. *Applies to adults.*
- Effects of Onsite Vegetation Management on Predators. This update replaces “Predators” with “Arthropod Assemblage” and “Vertebrate Assemblage.” *Applies to all life stages.*
- Effects of Onsite Visitation and Study on Competitors. As noted above, the original CEM (Braun 2015) included these two habitat elements for larvae and adults. This update drops both of these two habitat elements and, insofar as the original habitat elements concerned arthropods, replaces them with the broad category of arthropods. *Applies to larvae and adults.*
- Effects of Onsite Visitation and Study on Predators. This update replaces “Predators” with “Arthropod Assemblage” and “Vertebrate Assemblage.” *Applies to all life stages.*

## UPDATED LINKS WITH CONTROLLING FACTORS AS CAUSAL AGENTS

- Onsite Water Management effects on Soil Moisture (HE): The link reason is updated to state that the LCR MSCP manages water applications on MNSW habitat sites through the exercise of its water rights. Water applications are a crucial tool for managing soil moisture levels on MNSW habitat sites in the absence of natural groundwater and inundation dynamics. Conversely, a reduction or termination of water applications at a site also may affect soil moisture. Specifically, Ronning (2018) notes the following concerning the effects of soil moisture on quailbush, herbaceous vegetation, and woody vegetation in areas where soil moisture previously was sustained by irrigation but where irrigation has been curtailed: “We have reduced irrigation in a number of established honey mesquite patches in order to use the water in areas with cottonwood-willow land cover. Grasses have been reduced or died off and in some of the phases the quailbush appears to be showing stress (have more bare branches) and there is little to no quailbush recruitment except in the areas where soil moisture is available (along irrigation ditches that had water in them to irrigate other areas and edges of roads).” All other fields are unchanged. *Applies to all life stages.*

## NEW LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

- Chemical Contaminants effects on Arthropod Assemblage (HE): As noted above, this update drops the habitat elements, “Competitors” and “Predators,” and replaces them with two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage.” The present link replaces the original links to characterize the effects of chemical contaminants on arthropod competitors and predators. As noted above (see chapter 4), the LCR MSCP is authorized to use pesticides to manage insects in habitat conservation areas, and offsite land uses may entail application of pesticides that could drift onto MNSW habitat sites. Additionally, chemical residues may be present from past land uses at MNSW habitat sites on former farm lands. These circumstances at least raise the possibility of chemical contamination affecting the spectrum of arthropods present on MNSW habitat sites that could prey on MNSW or provide alternative food sources for birds or other animal taxa that might otherwise prey on MNSW. The hypothesized link is proposed to be complex and unidirectional but with unknown intensity, spatial scale, or temporal scale. The link magnitude reason notes that the proposed relationship is only a theoretical possibility. Little is known about the



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presence of chemical contaminants at MNSW sites and how these contaminants may affect MNSW or other arthropods. Link predictability therefore is unknown and link understanding low. *Applies to all life stages.*

- **Chemical Contaminants effects on Chemical Stress (CAP):** This update includes a new critical biological process, “Chemical Stress,” to better represent the ways in which chemical contaminants and extreme concentrations of natural chemical substances may affect MNSW in every life stage (see chapter 3). This new link replaces an original link from chemical contaminants to “Contamination and Infection,” focusing on the “contamination” part of the original link. The link reason notes that MNSW, as with all butterflies, are vulnerable to stress and mortality in every life stage due to exposure to harmful contaminants. Such contaminants potentially may disrupt insect health and/or impair growth, development, or reproduction. The hypothesized link is proposed to be positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of contaminants present, the greater the likelihood that MNSW will experience some form of chemical stress. The link is proposed to be unidirectional, with low intensity, low spatial scale, and low temporal scale. The link magnitude reason notes that the proposed relationship is only a theoretical possibility. There is not sufficient information to assess link magnitude because little is known about the presence of chemical contaminants at MNSW sites or how they affect MNSW. However, the literature reviewed and experts consulted for this CEM report no instances of even possible contamination leading to harm among MNSW. Link predictability is rated as unknown and link understanding low. *Applies to all life stages.*
- **Chemical Contaminants effects on Herbaceous Vegetation (HE):** The original CEM noted possible effects of chemical contaminants on competitors and on MNSW nectar sources. As noted above, this update drops “Competitors” as a habitat element, replacing it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. The link reason notes that all herbaceous plants are vulnerable to stress and mortality due to exposure to harmful contaminants. Such contaminants potentially may disrupt plant health and/or impair growth or reproduction. The hypothesized link is proposed to be positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of contaminants present, the greater the likelihood that herbaceous plants will experience some form of chemical stress. The link is proposed to be unidirectional, with low intensity, low spatial scale, and low temporal scale. The link magnitude reason notes that the proposed relationship is only a theoretical possibility. There is not sufficient information to assess

link magnitude because little is known about the presence of chemical contaminants at MNSW sites or how they affect the vegetation. However, the literature reviewed and experts consulted for this CEM report no instances of even possible contamination causing harm to any vegetation on MNSW sites. Link predictability is rated as unknown and link understanding low. *Applies to all life stages.*

- Chemical Contaminants effects on Vertebrate Assemblage (HE): As noted above, this update drops the habitat elements, “Competitors” and “Predators,” and replaces them with two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage.” The present link replaces the original links to characterize the effects of chemical contaminants on vertebrate competitors and predators. As noted above (see chapter 4), the LCR MSCP is authorized to use pesticides to manage insects in habitat conservation areas, and offsite land uses may entail application of pesticides that could drift onto MNSW habitat sites. Additionally, chemical residues may be present from past land uses at MNSW habitat sites on former farm lands. These circumstances at least raise the possibility of chemical contamination unintentionally affecting the spectrum of vertebrates present on MNSW habitat sites that could prey on MNSW or on arthropods that might otherwise prey on MNSW. The hypothesized link is proposed to be complex and unidirectional, but with unknown intensity, spatial scale, or temporal scale. The link magnitude reason notes that the proposed relationship is only a theoretical possibility. Little is known about the presence of chemical contaminants at MNSW sites or how these contaminants may affect any vertebrates that happen to come into contact with the contaminants. Link predictability therefore is unknown and link understanding low. *Applies to all life stages.*
- Chemical Contaminants effects on Woody Vegetation (HE): The original CEM noted possible effects of chemical contaminants on competitors and on MNSW nectar sources. As noted above, this update drops “Competitors” as a habitat element, replacing it with two broad categories of plants, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage,” and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. The link reason notes that all woody plants are vulnerable to stress and mortality due to exposure to harmful contaminants. Such contaminants potentially may disrupt plant health and/or impair growth or reproduction. The hypothesized link is proposed to be positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of contaminants present, the greater the likelihood that woody plants will experience some form of chemical stress. The link is proposed to be unidirectional, with low intensity, low spatial scale, and low temporal scale. The link magnitude reason notes that the proposed relationship is only a theoretical possibility. There is not sufficient information to assess link magnitude

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because little is known about the presence of chemical contaminants at MNSW sites or how they affect the vegetation. However, the literature reviewed and experts consulted for this CEM report no instances of even possible contamination causing harm to any vegetation on MNSW sites. Link predictability is rated as unknown and link understanding low.

*Applies to all life stages.*

- Fire Regime effects on Herbaceous Vegetation (HE): The original CEM noted possible effects of the fire regime on MNSW nectar sources and therefore addressed these effects only for the adult life stage. As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of fire on both herbaceous and woody vegetation (see below), and addresses these effects for all four life stages. The link reason notes that fire can greatly diminish or destroy patches of herbaceous vegetation but may also open habitat for colonization or reestablishment of the same or other herbaceous vegetation. Fire resistance and/or adaptations vary among the herbaceous species of the LCR ecosystem, including MNSW nectar sources. Arrowweed, which may be either herbaceous or a woody shrub depending on its age, is moderately fire resistant (USDA 2018). Sweetbush (*Bebbia juncea*), which also may be either herbaceous or a woody shrub depending on its age, appears to be able to recover from roots and/or seeds following fire (Brown and Minnich 1986). On the other hand, salt heliotrope, western purslane (*Sesuvium verrucosum*), alkali mallow, and common purslane (*Portulaca oleacea*) 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. The hypothesized link is proposed to be complex and bi-directional because the composition of the herbaceous vegetation assemblage reciprocally affects the fire regime. The link is proposed to have medium intensity, with high spatial and temporal scales. The link magnitude reason notes that the herbaceous plant species of the LCR ecosystem are fire-sensitive to varying degrees. As a result, the presence versus absence of fire and the intensity and timing of fire will have varying effects on the herbaceous vegetation assemblages in and around MNSW sites. In turn, the density of herbaceous vegetation in and around MNSW habitat sites may affect the frequency and severity of wildfire across these sites. Link predictability is rated as medium because the relationship is affected by multiple factors. Link understanding is rated as low: The principles of the relationship are well understood in general, but the relationship has not been studied

systematically specifically with respect to MNSW habitat and the herbaceous species of the LCR ecosystem, including MNSW nectar sources. *Applies to all life stages.*

- **Fire Regime effects on Woody Vegetation (HE):** The original CEM noted possible effects of the fire regime on MNSW nectar sources and therefore addressed these effects only for the adult life stage. As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of fire on both herbaceous and woody vegetation (see below), and addresses these effects for all four life stages. The link reason notes that fire can greatly diminish or destroy patches of woody vegetation but may also open habitat for colonization or reestablishment of the same or other woody vegetation. Fire resistance and/or adaptations vary among the woody species of the LCR ecosystem, including 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, 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). Arrowweed, which may be either herbaceous or a woody shrub depending on its age, as noted above, is moderately fire resistant (USDA 2018). Sweetbush, which also may be either herbaceous or a woody shrub depending on its age, appears to be able to recover from roots and/or seeds following fire (Brown and Minnich 1986). The hypothesized link is proposed to be complex and bi-directional because the composition of the woody vegetation assemblage reciprocally affects the fire regime. The link is proposed to have medium intensity, with high spatial and temporal scales. The link magnitude reason notes that the woody plant species of the LCR ecosystem are fire-sensitive to varying degrees. As a result, the presence versus absence of fire and the intensity and timing of fire will have varying effects on the herbaceous vegetation assemblages in and around MNSW sites. In turn, the density of woody vegetation in and around MNSW habitat sites may affect the frequency and severity of wildfire across these sites. Link predictability is rated as medium because the relationship is affected by multiple factors. Link understanding is rated as medium: The principles of the relationship are well understood in general, and the fire-related dynamics of both saltcedar and mesquite have been well studied, although not specifically with respect to MNSW habitat and the woody species of the LCR ecosystem. *Applies to all life stages.*
- **Herbaceous Vegetation Assemblage effects on the Arthropod Assemblage (HE):** The original CEM noted possible effects of MNSW nectar sources

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on arthropods as competitors with MNSW for these sources and therefore addressed these effects only for the adult life stage. As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of herbaceous and woody vegetation (see below) on the arthropod assemblage, and addresses these effects for all four life stages. As noted in chapter 4, numerous arthropods occur in the herbaceous plant communities of the LCR ecosystem, and the species richness and abundance of these arthropods generally appears to correlate with the species richness and abundance of the herbaceous plant assemblage. In turn, these arthropods include pollinators and herbivores, the activities of which reciprocally must affect the species richness and abundance of the herbaceous plant assemblage. The link therefore is proposed to be bi-directional and, given the wide range of ecological interactions involved, necessarily complex. The link is proposed to have high intensity, spatial scale, and temporal scale. Link predictability is rated as medium: While the general relationship between plant and arthropod diversity is predictable, specific relationships between particular plant and particular arthropods are not understood well enough to assume predictability. *Applies to all life stages.*

- **Herbaceous Vegetation Assemblage effects on Quailbush Patch Size and Structure (HE):** This update identifies two broad categories of plants, herbaceous and woody vegetation. Individual quailbush plants are herbaceous when young but become woody as they grow into shrubs. Other herbaceous plants may compete with quailbush to become established at a newly available (e.g., disturbed) location and may also compete for water and nutrients once established, thereby affecting and being affected by quailbush patch size and structure. The hypothesized link is proposed to be bi-directional and complex: Individual quailbush and other plants necessarily interact in complex ways, affecting each other's access to space, shade, water, and nutrients, and thereby affecting and being affected by quailbush patch size and structure. The link is proposed to have unknown intensity, because the interactions are poorly studied, and to have medium spatial and temporal scales because they presumably apply only during the early stages of quailbush growth, before the individual plants become woody shrubs that dominate over herbaceous vegetation. Link predictability is unknown and link understanding low, because the interactions are poorly studied, even if expectable in general. *Applies to all life stages.*
- **Herbaceous Vegetation Assemblage effects on the Vertebrate Assemblage (HE):** As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation. The original CEM recognized but did not substantially address the ways in which the vegetation in and

around MNSW sites may affect the types and abundances of vertebrates that may visit or occur in MNSW sites, or where they may feed on the herbaceous vegetation or prey on MNSW and other arthropods (see below). This update therefore addresses the effects of herbaceous and woody vegetation (see below) on the vertebrate assemblage, and addresses these effects for all four life stages. As noted in the updates to chapter 4, numerous vertebrates visit or occur in the herbaceous plant communities of the LCR ecosystem, including birds, both large and small mammals, reptiles, and amphibians. The species richness and abundance of at least the birds generally appears to correlate with the species richness and abundance of the herbaceous plant assemblage apparently because of the richness of the associated arthropod assemblage. The link is proposed to be unidirectional and, given the wide range of ecological interactions involved, necessarily complex. The link is proposed to have high intensity, spatial scale, and temporal scale. Link predictability is rated as medium: While the general relationship between plant and vertebrate diversity is predictable, specific relationships between particular plant and particular vertebrates are not understood well enough to assume predictability. *Applies to all life stages.*

- Inundation Regime effects on the Herbaceous Vegetation Assemblage (HE): The original CEM (Braun 2015) recognized that the inundation regime not only can affect quailbush patches, but can also affect MNSW nectar sources, and recognized this causal relationship specifically for the adult life stage. As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of the inundation regime on both herbaceous and woody vegetation (see below), and addresses these effects for all four life stages. The link reason notes that inundation of sufficient duration can damage or destroy patches of herbaceous vegetation by suffocating plant roots, but such disturbances may also open up habitat for colonization or reestablishment of the same or other herbaceous species. On the other hand, inundation of brief duration may only cause temporary stress to herbaceous plants and provide crucial soil moisture, and herbaceous species vary in their sensitivity to effects of prolonged root inundation. For example, salt heliotrope and arrowweed (which is either herbaceous or woody depending on plant age) tolerate flooding and recover quickly. Many herbaceous species also presumably can reseed quickly (see effects of fire on herbaceous species in [Braun 2015]). The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. The link is proposed to have low intensity, spatial scale, and temporal scale: Inundation occurs only rarely at quailbush patches in the LCR ecosystem, with limited duration and little depth, and subsequent weather conditions

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can quickly dry out the soil again; perennial herbaceous plant numbers may recover quickly from soil seed banks and/or seeding from nearby stands. Link predictability is low due to the large number of variables involved. Link understanding is medium because the principles of this relationship are very well understood in general, although the relationship has not been studied systematically specifically within MNSW habitat. *Applies to all life stages.*

- Inundation Regime effects on the Woody Vegetation Assemblage (HE): The original CEM (Braun 2015) recognized that the inundation regime not only can affect quailbush patches but can also affect MNSW nectar sources, and recognized this causal relationship specifically for the adult life stage. As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of the inundation regime on both herbaceous (see above) and woody vegetation, and addresses these effects for all four life stages. The link reason notes that inundation of sufficient duration can damage or destroy patches of woody vegetation by suffocating plant roots, but such disturbances may also open up habitat for colonization or reestablishment of the same or other woody species. On the other hand, inundation of brief duration may only cause temporary stress to woody plants and provide crucial soil moisture, and woody species vary in their sensitivity to effects of prolonged root inundation. For example, saltcedar, arrowweed (which is either herbaceous or woody depending on plant age), and mesquite (although the latter to a slightly lesser extent) tolerate flooding and recover quickly. Many woody species also presumably can regenerate quickly (see effects of fire on woody species Braun [2015]). The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. The link is proposed to have low intensity, spatial scale, and temporal scale: Inundation occurs only rarely in areas with or surrounding quailbush patches in the LCR ecosystem, with limited duration and little depth, and subsequent weather conditions can quickly dry out the soil again; woody vegetation may recover quickly from surviving roots and trunks. Link predictability is low due to the large number of variables involved. Link understanding is medium because the principles of this relationship are very well understood in general, although the relationship has not been studied systematically specifically within MNSW habitat. *Applies to all life stages.*
- Quailbush Patch Distribution effects on the Vertebrate Assemblage (HE): The distribution of quailbush patches across the LCR landscape affects the distribution or movements of vertebrates that may feed on the plant, use the plant as cover, or feed on arthropods or other fauna (e.g., smaller

vertebrates) that may occur in quailbush patches. The affected vertebrates include birds, mammals, reptiles, and amphibians, as discussed in the updates to chapter 4, (see “Vertebrate Assemblage”). The hypothesized link is proposed to be bi-directional, because vertebrate herbivory on quailbush could affect its distribution, and complex because the cause and effect node both include several variables with complex interactions. The link is proposed to have low intensity but high spatial and temporal scale: Other factors likely have greater influence on the distribution and movements of vertebrates across the landscape, but to the extent that quailbush patch distribution is one of these factors, its effects will be widespread and year round. Link predictability is low for the same reasons. Link understanding is low: The principles of this relationship are very well understood in general, but the relationship has not been studied systematically within the LCR ecosystem. *Applies to all life stages.*

- Quailbush Patch Size and Structure Effects on the Arthropod Assemblage (HE): Quailbush patch size and structure, including the vertical and horizontal size of individual shrubs, their spatial proximity to each other (shrub density), and the overall spatial extent of each cluster of shrubs, affect the composition and abundance of arthropods within each such cluster. The greater the size, shrub density, and volume of quailbush vegetation within a cluster, the greater the abundance of arthropods that the cluster can support, including species that use the vegetation as cover, feed on the vegetation, or feed on other arthropods that use the vegetation. The hypothesized link is proposed to be bi-directional, because arthropod herbivory on quailbush could affect its distribution, and complex because the cause and effect node both include several variables with complex interactions. The link is proposed to have medium intensity but high spatial and temporal scale: Other factors likely also affect the arthropod assemblage within individual quailbush patches, but the effects of patch size and structure will be widespread and year round. Link predictability is medium for the same reasons. Link understanding is medium: The principles of this relationship are very well understood in general, and arthropod data collected by the LCR MSCP appear to support the hypothesis, but the data have not been systematically analyzed. *Applies to all life stages.*
- Quailbush Patch Size and Structure Effects on the Vertebrate Assemblage (HE): This link hypothesizes that quailbush patch size and structure, including the vertical and horizontal size of individual shrubs, their spatial proximity to each other (shrub density), and the overall spatial extent of each cluster of shrubs, affect the composition and abundance of vertebrates that occur within or visit each such cluster. The greater the size, shrub density, and volume of quailbush vegetation within a cluster, the greater the diversity of vertebrates that may feed on the plants in a cluster, use the plants as cover, or feed on arthropods or other fauna



(e.g., smaller vertebrates) that may occur in the cluster. However, some vertebrates may be deterred from using clusters with high density: LCR MSCP investigators report that clusters with high density are difficult to penetrate during surveys—presumably by people of normal adult size. The affected vertebrates may include birds, mammals, reptiles, and amphibians, as discussed in the updates to chapter 4 (see “Vertebrate Assemblage”). The hypothesized link is proposed to be bi-directional, because vertebrate herbivory on quailbush could affect its patch size and structure, and complex because the cause and effect node both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects of patch size and structure will be widespread and year round. Link predictability is unknown, and link understanding is low for the same reason. *Applies to all life stages.*

- Quailbush Shrub Condition effects on the Arthropod Assemblage (HE): Quailbush shrub condition, including the vertical and horizontal size of the individual shrub, its lushness, and the nutritional content of its leaves and seeds, affect the composition and abundance of arthropods that the shrub can support, including species that use the vegetation as cover, feed on the vegetation, or feed on other arthropods that use the vegetation. The composition and abundance of the arthropods within a shrub that feed on shrub leaves or fluids, reciprocally, presumably will, in turn, affect shrub condition. The hypothesized link is proposed to be bi-directional, because arthropod herbivory on quailbush could affect quailbush condition, and complex, because the cause and effect node both include several variables with complex interactions. The link is proposed to have medium intensity but high spatial and temporal scale: Other factors likely also affect the arthropod assemblage within individual quailbush shrubs, but the effects of shrub condition will be widespread and year round. Link predictability is medium for the same reasons. Link understanding is medium: The principles of this relationship are very well understood in general, and arthropod data collected by the LCR MSCP appear to support the hypothesis, but the data have not been systematically analyzed. *Applies to all life stages.*
- Quailbush Shrub Condition effects on the Vertebrate Assemblage (HE): Quailbush shrub condition, including the vertical and horizontal size of the individual shrub, its lushness, and the nutritional content of its leaves and seeds, affect the composition and abundance of vertebrates that may feed on the shrub and/or possibly that use the shrub as cover or feed on arthropods or other fauna (e.g., smaller vertebrates) that may occur on the shrub. The affected vertebrates may include birds, mammals, reptiles, and amphibians, as discussed in the updates to chapter 4, “Vertebrate Assemblage.” The composition and abundance of vertebrates that may

feed on the shrub, reciprocally, presumably can affect shrub condition. The hypothesized link is proposed to be bi-directional because vertebrate herbivory on quailbush could affect quailbush condition, and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects will be widespread and year round. Link predictability is unknown, and link understanding is low for the same reason. *Applies to all life stages.*

- Soil Moisture effects on the Herbaceous Vegetation Assemblage (HE): Soil moisture conditions presumably affect the availability, quality, and spatial distribution of herbaceous vegetation within and around quailbush patches. For example, salt heliotrope can dry up entirely under drought 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 (LCR MSCP 2013). However, the literature reviewed for this CEM does not systematically address the ways in which soil moisture may affect herbaceous vegetation density, spatial distributions, or the quantity or quality of nectar some of them produce. The hypothesized link is proposed to be unidirectional and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects will be widespread and year round. The hypothesis is consistent with the experience of MNSW investigators, and LCR MSCP field investigations of MNSW sites are accumulating data with which the hypothesis might be assessed. Link predictability is unknown, and link understanding is low, for the same reason. *Applies to all life stages.*
- Soil Moisture effects on the Woody Vegetation Assemblage (HE): Soil moisture conditions presumably can affect the availability, quality, and spatial distribution of woody vegetation within and around quailbush patches. However, the woody species present in and around quailbush patches in the LCR ecosystem are adapted to low soil moisture and, once established, are able to extend their roots to depths inaccessible to herbaceous plants (Meyer 2005; Steinberg 2001; Zouhar 2003). In any case, the literature reviewed for this CEM does not systematically address the ways in which soil moisture may affect woody vegetation density, spatial distributions within or surrounding MNSW sites, or the quantity or quality of nectar some of them produce. The hypothesized link is proposed to be unidirectional and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects will

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be widespread and year round. The hypothesis is consistent with the experience of MNSW investigators, and LCR MSCP field investigations of MNSW sites are accumulating data with which the hypothesis might be assessed. Link predictability is unknown, and link understanding is low, for the same reason. *Applies to all life stages.*

- Soil Nitrogen effects on the Herbaceous Vegetation Assemblage (HE): Soil nitrogen conditions should be expected to affect the availability, quality, and spatial distribution of herbaceous vegetation in and around quailbush patches. However, the literature reviewed for this CEM does not systematically address this topic. In addition, Nelson et al. (2015), Pratt and Wiesenborn (2009), Wiesenborn (2010a, 2010b), and Wiesenborn and Pratt (2010) suggest that MNSW adults prefer nectar with higher concentrations of amino acids, which in turn contribute to adult MNSW condition. If herbaceous nectar sources vary in amino acid production in their nectar, it is possible that variation in soil nitrogen levels contribute to that variation. The hypothesized link is proposed to be unidirectional and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects will be widespread and year round. Link predictability is unknown. Link understanding is low: The principles of this relationship are well understood in general, but the relationship has not been studied specifically in the LCR ecosystem. *Applies to all life stages.*
- Soil Nitrogen effects on the Woody Vegetation Assemblage (HE): Soil nitrogen conditions should be expected to affect the availability, quality, and spatial distribution of herbaceous vegetation in and around quailbush patches. 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 (Steinberg 2001), and as with quailbush, its condition therefore may not be sensitive to soil nitrogen levels. The literature reviewed for this CEM does not otherwise address this topic. Nelson et al. (2015), Pratt and Wiesenborn (2009), Wiesenborn (2010a, 2010b), and Wiesenborn and Pratt (2010) suggest that MNSW adults prefer nectar with higher concentrations of amino acids, which in turn contribute to adult MNSW condition. If woody nectar sources vary in amino acid production in their nectar, it is possible that variation in soil nitrogen levels contribute to that variation. The hypothesized link is proposed to be unidirectional and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale:

The relationship has not been evaluated with field data, but the effects will be widespread and year round. Link predictability is unknown. Link understanding is low: The principles of the relationship are well understood in general, but the relationship has not been studied specifically in the LCR ecosystem. *Applies to all life stages.*

- Soil Salinity effects on the Herbaceous Vegetation Assemblage (HE): Soil salinity conditions presumably affect the availability, quality, and spatial distribution of herbaceous vegetation in and around quailbush patches. With the exception of sweetbush, all of the native herbaceous nectar sources used by MNSW tolerate or prefer soils with high salinity (USDA 2018). Other herbaceous plants that occur alongside these native herbaceous nectar source plants therefore presumably also tolerate or prefer such soils. However, the literature reviewed for this CEM does not systematically address this topic. The hypothesized link is proposed to be unidirectional and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects will be widespread and year round. Link predictability is unknown. Link understanding is low: The principles of the relationship are well understood in general, but the relationship has not been studied specifically in the LCR ecosystem. *Applies to all life stages.*
- Soil Salinity effects on the Woody Vegetation Assemblage (HE): Soil salinity conditions presumably affect the availability, quality, and spatial distribution of woody vegetation in and around quailbush patches. All of the woody nectar sources used by MNSW—both of the two native mesquite species (Steinberg 2001), the native arrowweed, and the non-native saltcedar (Zouhar 2003; Nagler et al. 2011)—tolerate or prefer soils with high salinity (USDA 2018). Other woody plants that occur alongside these native woody nectar source plants therefore presumably also tolerate or prefer such soils. However, the literature reviewed for this CEM does not systematically address this topic. The hypothesized link is proposed to be unidirectional and complex because the cause and effect nodes both include several variables with complex interactions. The link is proposed to have unknown intensity but high spatial and temporal scale: The relationship has not been evaluated with field data, but the effects will be widespread and year round. Link predictability is unknown. Link understanding is low: The principles of the relationship are well understood in general, but the relationship has not been studied specifically in the LCR ecosystem. *Applies to all life stages.*
- Woody Vegetation Assemblage effects on the Arthropod Assemblage (HE): The original CEM noted possible effects of MNSW nectar sources on arthropods as competitors with MNSW for these sources and therefore

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addressed these effects only for the adult life stage. As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of herbaceous and woody vegetation (see below) on the arthropod assemblage and addresses these effects for all four life stages. As noted in chapter 4, numerous arthropods occur in the plant communities of the LCR ecosystem, and the species richness and abundance of these arthropods generally appears to correlate with the species richness and abundance of the plant assemblage. In turn, these arthropods include pollinators and herbivores, the activities of which reciprocally must affect the species richness and abundance of the plant assemblage. The northern tamarisk beetle, in particular, has a strong negative effect on saltcedar condition and abundance. The link therefore is proposed to be bi-directional and, given the wide range of ecological interactions involved, necessarily complex. The link is proposed to have high intensity, spatial scale, and temporal scale. Link predictability is rated as medium: While the general relationship between plant and arthropod diversity is predictable, specific relationships between particular plant and particular arthropods other than between saltcedar and the northern tamarisk beetle are not studied or understood well enough to assume predictability. *Applies to all life stages.*

- **Woody Vegetation Assemblage effects on Quailbush Patch Distribution (HE):** Woody vegetation across the larger landscape (including quailbush patches) defines the corridors available for MNSW dispersal and the gaps they need to overfly. Areas cleared of the non-native woody saltcedar may also provide opportunities for colonization by quailbush. Reciprocally, quailbush is a component of the woody vegetation assemblage. The hypothesized link is proposed to be bi-directional and complex: Quailbush and the other woody species of the LCR ecosystem necessarily interact in complex ways, affecting each other's access to space, shade, water, and nutrients, thereby affecting and being affected by quailbush patch distribution. The link is proposed to have unknown intensity, because the interactions are poorly studied, and to have medium spatial and temporal scales because they presumably apply only during the early stages of quailbush growth, during the process of becoming established—or not—within the existing plant matrix of the landscape. Link predictability is unknown, and link understanding low, because the interactions are poorly studied, even if expectable in general. *Applies to all life stages.*
- **Woody Vegetation Assemblage effects on Quailbush Patch Size and Structure (HE):** This update identifies two broad categories of plants, herbaceous and woody vegetation. Individual quailbush plants are herbaceous when young but become woody as they grow into shrubs.

Other woody plants may compete with quailbush to become established at a newly available (e.g., disturbed) location and may also compete for water and nutrients once established, thereby affecting and being affected by quailbush patch size and structure. The hypothesized link is proposed to be bi-directional and complex: Individual quailbush and other plants necessarily interact in complex ways, affecting each other's access to space, shade, water, and nutrients, and thereby affecting and being affected by quailbush patch size and structure. The link is proposed to have unknown intensity, because the interactions are poorly studied, and to have medium spatial and temporal scales because they presumably apply only during the early stages of quailbush growth, during the process of becoming established—or not—within the existing plant matrix of the landscape. Link predictability is unknown and link understanding low, because the interactions are poorly studied, even if expectable in general. *Applies to all life stages.*

- **Woody Vegetation Assemblage effects on the Vertebrate Assemblage (HE):** As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation. The original CEM recognized but did not substantially address the ways in which the vegetation in and around MNSW sites may affect the types and abundances of vertebrates that may visit or occur in MNSW sites, where they may feed on the woody vegetation (see competition) or prey on MNSW and other arthropods (see predation, competition). This update therefore addresses the effects of herbaceous (see above) and woody vegetation on the vertebrate assemblage and addresses these effects for all four life stages. As noted in chapter 4, numerous vertebrates visit or occur in the plant communities of the LCR ecosystem, including birds, both large and small mammals, reptiles, and amphibians. The species richness and abundance of at least the birds generally appears to correlate with the species richness and abundance of the plant assemblage apparently because of the richness of the associated arthropod assemblage. The link is proposed to be bi-directional, because vertebrate herbivory on woody vegetation could affect the composition and structure of such vegetation, and given the wide range of ecological interactions involved, necessarily complex. The link is proposed to have high intensity, spatial scale, and temporal scale. Link predictability is rated as medium: While the general relationship between plant and vertebrate diversity is predictable, specific relationships between particular plant and particular vertebrates are not studied or understood well enough to assume predictability. *Applies to all life stages.*

## DELETED LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS

- Effects of Chemical Contaminants on Competitors for larvae and adults. This update replaces “Competitors” with “Arthropod Assemblage” and “Vertebrate Assemblage,” and also with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” insofar as “Competitors” refers to plants. *Applies to Larvae and Adults.*
- Effects of Chemical Contaminants on Contamination and Infection. This update replaces “Contamination and Infection” with two separate critical processes, “Chemical Stress” and “Disease.” *Applies to all life stages.*
- Effects of Chemical Contaminants on Nectar Sources. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to adults.*
- Effects of Chemical Contaminants on Predators. This update replaces “Predators” with “Arthropod Assemblage” and “Vertebrate Assemblage.” *Applies to all life stages.*
- Effects of Competitors on Hiding/Resting. This update replaces “Competitors” with “Arthropod Assemblage” and “Vertebrate Assemblage,” and also with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” insofar as “Competitors” refers to plants. *Applies to larvae and Adults.*
- Effects of Competitors on Nectar Sources. This update replaces “Competitors” with “Arthropod Assemblage” and “Vertebrate Assemblage,” and also with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” insofar as “Competitors” refers to plants, and replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to Adults.*
- Effects of Competitors on Quailbush Shrub Condition. This update replaces “Competitors” with “Arthropod Assemblage” and “Vertebrate Assemblage,” and also with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” insofar as “Competitors” referred to plants. *Applies to Larvae and Adults.*
- Effects of Fire Regime on Nectar Sources. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to Adults.*

## Updates to Chapter 6 – Conceptual Ecological Model by Life Stage

- Effects of Infectious Agents on Contamination and Infection. This update replaces “Contamination and Infection” with two separate critical processes, “Chemical Stress” and “Disease.” *Applies to all life stages.*
- Effects of Inundation Regime on Nectar Sources. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to Adults.*
- Effects of Inundation Regime on Physiological Stress. This update divides and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” *Applies to all life stages.*
- Effects of Monitoring, Capture, Handling on Physiological Stress. This update divides and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” *Applies to all life stages.*
- Effects of Nectar Sources on Feeding/Watering. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to Adults.*
- Effects of Quailbush Litter Condition on Predators. This update replaces “Predators” with “Arthropod Assemblage” and “Vertebrate Assemblage,” which may live in the litter during MNSW egg and pupal stages as well as during larval and adult stages. *Applies to Pupae, Larvae, and Adults (original CEM did not include this link for Eggs).*
- Effects of Quailbush Patch Size and Structure on Physiological Stress. This update divides and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” *Applies to all life stages.*
- Effects of Quailbush Patch Size and Structure on Predators. This update replaces “Predators” with “Arthropod Assemblage” and “Vertebrate Assemblage.” *Applies to all life stages.*
- Effects of Quailbush Shrub Condition on Physiological Stress. This update divides and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” *Deletion applies to Eggs, Larvae, and Pupae; addressing of effects in CEM update applies to all life stages.*
- Effects of Quailbush Shrub Condition on Predators. This update replaces “Predators” with “Arthropod Assemblage” and “Vertebrate Assemblage.” *Applies to all life stages.*
- Effects of Soil Moisture on Nectar Sources. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to Adults.*



- Effects of Soil Nitrogen on Nectar Sources. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage” *Applies to Adults*.
- Effects of Soil Salinity on Nectar Sources. This update replaces “Nectar Sources” with “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” *Applies to adults*.

## **UPDATED LINKS WITH HABITAT ELEMENTS AS CAUSAL AGENTS**

- Arthropod Assemblage effects on Competition (CAP): As noted above, this update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, herbaceous and woody vegetation, and two broad categories of animals, arthropods and vertebrates. This update also adds the critical biological process, “Competition,” to capture the ways in which arthropods and vertebrates affect the rate of competition experienced by MNSW for habitat and food resources as larvae and adults. (Competition also covers the ways in which other plants compete with quailbush for water and space, discussed below). The link reason notes: (1) MNSW larvae may face competition for quailbush leaf resources from at least two Lepidoptera species that also use quailbush as a larval host plant, the saltbush sootywing (*H. alpheus*) and the western pygmy blue (*B. exilis*) (see chapter 4, “Arthropod Assemblage”). (2) MNSW adults may face competition from perhaps dozens of Lepidoptera for its nectar sources, let alone from other arthropods that may feed on these same plants or their nectar (see table 3). For both larval and adult MNSW, changes in the arthropod assemblage would be expected to result in changes in the types and intensities of competition that the MNSW face. The link is hypothesized to be positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of arthropods present, the greater the competition MNSW larvae or adults will face from other arthropods. The link is hypothesized to be bi-directional because MNSW are themselves part of the overall arthropod assemblage. The link is proposed to have unknown intensity and high spatial and temporal scales, with unknown link predictability and low understanding. *Applies to Larvae and Adults*.
- Arthropod Assemblage effects on Predation (CAP): As noted above, this update drops the habitat element, “Predators,” and replaces it with two broad categories of animals, arthropods and vertebrates, and recognizes that MNSW in all life stages can experience predation from arthropods.

This update notes that a wide range of arthropods are known to prey on butterflies in all life stages, in general. The general literature particularly notes that spiders, ants, wasps, dragonflies, robber flies, crickets, and mantises may prey on butterflies. Mantises would hunt in the foliage; spiders would be expected to hunt and trap both within the foliage and within the leaf litter beneath quailbush shrubs; and ants would be expected to hunt larvae in the foliage. However, there are no published reports of arthropods preying on MNSW, in any life stage, apparently because the topic has not been studied. Nevertheless, changes in the arthropod assemblage would be expected to result in changes in the types and intensities of predation that MNSW face. The link is hypothesized to be positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of arthropods present, the greater the predation MNSW in all life stages will experience from other arthropods. The link is hypothesized to be bi-directional because MNSW are themselves part of the overall arthropod assemblage. The link is proposed to have unknown intensity and high spatial and temporal scales, with unknown link predictability and low understanding. *Applies to all life stages.*

- **Herbaceous Vegetation Assemblage effects on Foraging (CAP):** The original CEM noted possible effects of MNSW nectar sources on adult feeding/watering (renamed “foraging” in this update). As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of herbaceous and woody vegetation (see below) on adult foraging separately. The link reason notes that MNSW adults feed on nectar from a range of herbaceous and woody plants, as discussed in the chapter 3, “Foraging,” and chapter 4, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” The types, distribution, and condition of nectar sources available within the herbaceous vegetation assemblage in and around MNSW sites, and their variation over time, therefore affect the amount of energy that MNSW adults must expend to obtain nectar, the distances and time they must fly to reach nectar sources, and the amount of sugar and other nutrients that they are able to obtain during feeding. The hypothesized link is proposed to be unidirectional and complex: The causal node and/or effect node include(s) several variables, and the effects of the former on the latter therefore are necessarily complex. The link is proposed to have high intensity, spatial scale, and temporal scale, with high predictability and high understanding. The link understanding reason notes: Relative to other topics concerning MNSW, this hypothesized relationship is comparatively well studied. Gaps in knowledge remain, however (e.g., how MNSW select among alternative potential sources based on the food quality, availability, and spatial distribution of these sources and how

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far MNSW will travel in search of nectar during periods of scarcity).  
*Applies to Adults.*

- Infectious Agents effects on Disease (CAP): The original CEM (Braun 2015) combined contamination and infection (disease) in a single category of critical biological processes. This update separates that single category into its two parts. The link reason notes simply that infectious agents cause disease. The hypothesized link is proposed to be unidirectional and to involve a positive relationship, with no threshold, on the assumption that the incidence of disease among MNSW will vary at least, in part, with the diversity and abundance of infectious agents present. The link is proposed to have low intensity and unknown spatial and temporal scales: The proposed relationship is theoretically likely, but there is little or nothing known about the presence of infectious agents at MNSW sites or how they affect MNSW. However, the literature reviewed and experts consulted for this CEM report no instances of even possible infections leading to harm among MNSW. Link predictability is rated as unknown and link understanding low. *Applies to all life stages.*
- Inundation Regime effects on Mechanical Stress (CAP): The original CEM (Braun 2015) addressed mechanical stress under the broader category of physiological stress. This update separates that same category into two parts, mechanical and thermal stress. The link reason notes that MNSW in all four life stages presumably experience mechanical stress if inundated even briefly—and die if inundated too long. However, the literature provides no information on whether or how long MNSW in any life stage can tolerate complete wetting. The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. It is proposed to have unknown intensity and low spatial and temporal scales: Inundation occurs only rarely in MNSW habitat sites, with limited duration and little depth, and subsequent weather conditions can quickly dry MNSW sites out again. Consequently, inundation events of sufficient duration and depth do harm MNSW. However, the incidence and effects of inundation on MNSW in any life stage have not been studied. *Applies to all life stages.*
- Monitoring, Capture, Handling effects on Mechanical Stress (CAP): As noted above, the original CEM (Braun 2015) addressed mechanical stress under the broader category of physiological stress. This update separates that same category into two parts, mechanical and thermal stress. MNSW in all four life stages presumably experience mechanical stress if captured and handled improperly. However, all the literature reviewed on this topic for this CEM concerns capture and handling of adult MNSW, not MNSW eggs, larvae, or pupae. Some field methods are known or suspected to harm MNSW adults. Nelson et al. (2015) describe and cite a supporting

study that field methods such as capture, mark, and recapture techniques can have “adverse effects” on butterflies, particularly on small-winged species such as MNSW. Consequently, recent LCR MSCP field monitoring of MNSW population status (Nelson et al. 2015) has collected 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 monitoring, capture, or handling even on MNSW adults. For example, Pratt and Wiesenborn report several studies involving handling of MNSW in the laboratory or the field but do not report on the incidence of any resulting harm or its absence (e.g., Pratt and Wiesenborn 2009; Wiesenborn 1999, 2010a). However, this lack of report of harm is consistent with findings by Willis et al. (2009), who report on the results of an experiment in artificial relocation (assisted colonization) with adults of two skipper species in the United Kingdom. The authors explicitly note that the adult skippers were netted, caged, transported, and released with no reported harm. The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. It is proposed to have unknown intensity, spatial scale, and temporal scale for eggs, larvae, and pupae, and low intensity, spatial scale, and temporal scale for adults: There are not sufficient studies or data available to assess any aspect of link magnitude for eggs, larvae, and pupae. The literature for adults indicates that, with careful selection, methods for capture and handling need not cause sufficient stress to MNSW to be a matter of concern to investigations of MNSW ecology. Link predictability consequently is unknown for eggs, larvae, and pupae, and high for adults. Link understanding consequently is low for eggs, larvae, and pupae, and medium for adults. *Applies to all life stages.*

- **Quailbush Patch Size and Structure effects on Mechanical Stress (CAP):** The original CEM (Braun 2015) addressed thermal stress under the broader category of physiological stress. This update separates that same category into two parts, mechanical and thermal stress. The spacing of quailbush shrubs within a patch and the overall size of the patch affect the extent to which MNSW eggs, larvae, pupae, and adults are sheltered versus exposed to stress from elevated winds in general, and the extent to which MNSW adults are sheltered versus exposed to stress from elevated winds while patrolling for mates or suitable locations for ovipositing. The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. It is proposed to have medium intensity and high spatial and temporal scales. MNSW eggs, larvae, and pupae have no means for using quailbush patch size and structure to help them avoid mechanical stress, and patch size and structure will affect their exposure to such stress. MNSW adults clearly avoid exposure to elevated windspeeds by flying close to the ground if they must cross open spaces in the wind and

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otherwise by sheltering in quailbush foliage (Nelson et al. 2014, 2015; Pratt and Wiesenborn 2011). Patch size and structure determine the extent of opportunities for such sheltering behavior among adults. The relationship has been observed but not systematically studied, and it is unlikely that the LCR MSCP program has data with which it could assess this hypothesis because it may be very difficult to assess stress levels in any MNSW life stage. Otherwise, the hypothesis rests on simple logic and information on MNSW adult interactions with wind (Pratt and Wiesenborn 2011; Nelson et al. 2014, 2015). The link has unknown predictability, because of the number of factors involved, and medium understanding based on a small number of observations. *Applies to all life stages.*

- **Quailbush Patch Size and Structure effects on Thermal Stress (CAP):** The original CEM (Braun 2015) addressed thermal stress under the broader category of physiological stress. This update separates physiological stress into two parts, mechanical and thermal stress. The spacing of quailbush shrubs within a patch, the overall size of the patch, and the presence of trees within or immediately around the patch affect the shading provided by the patch as a whole (versus shading provided by individual shrubs). This shading provides a crucial buffer for MNSW eggs, larvae, pupae, and adults from stress from elevated air temperatures. Specifically, 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 patches that incorporate or lie adjacent to trees, the shade of which may provide some additional protection against the heat (J. Hill and C. Ronning 2018, joint personal communication; Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 1997). The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. It is proposed to have medium intensity and high spatial and temporal scales. MNSW eggs and pupae have no means for using quailbush patch size and structure to help them avoid thermal stress, and patch size and structure will affect their exposure to such stress. MNSW larvae are mobile, but no reports appear to document larval movement within quailbush canopy other than into and out of their leaf shelters. MNSW adults clearly avoid exposure to elevated air temperatures not only in their use of shade but in their avoiding flying during the hottest hours of the day. Patch size and structure determine the extent of opportunities for such shade for adults. Otherwise, the hypothesis rests on simple logic and information on MNSW adult interactions with shade (see above). The link has unknown predictability because of the number of factors involved and medium understanding based on a small number of observations. *Applies to all life stages.*

- Quailbush Shrub Condition effects on Resting/Hiding (CAP): The link reason, link predictability reason, and link understanding reason are all updated for MNSW adults with the addition of the following statement: Ronning (2018) also notes, “...not all surface-type preferences for MNSW basking are known. It is also unknown if a lack or limited amount of their preferred basking surfaces affects presence or [vegetation] uses.” All other fields remain unchanged. *Applies only to Adults.*
- Quailbush Shrub Condition effects on Thermal Stress (CAP): The original CEM (Braun 2015) addressed thermal stress under the broader category of physiological stress. This update separates physiological stress into two parts, mechanical and thermal stress. The vertical and horizontal size, foliage density, and possibly foliage lushness of an individual quailbush shrub presumably all contribute to the shading effect of the shrub for MNSW. This shading provides a crucial buffer for MNSW eggs, larvae, pupae, and adults from stress from elevated air temperatures. Specifically, 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). The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. It is proposed to have medium intensity and high spatial and temporal scales. Foliage condition presumably affects the amount of shade on MNSW eggs and pupae, but these life stages have no means for moving to take advantage of variation in foliage density to help them avoid thermal stress. MNSW larvae are mobile, but no reports appear to document larval movement within quailbush canopy other than into and out of their leaf shelters. MNSW adults clearly avoid exposure to elevated air temperatures not only in their use of shade but in their avoiding flying during the hottest hours of the day. Shrub canopy quality helps determine the extent of opportunities for such shade for adults. Otherwise, the hypothesis rests on simple logic and information on MNSW adult interactions with shade (see above). The link has unknown predictability because of the number of factors involved and medium understanding based on a small number of observations. *Applies to all life stages.*
- Vertebrate Assemblage effects on Competition (CAP): As noted above, this update drops the habitat element, “Competitors,” and replaces it with two broad categories of plants, herbaceous and woody vegetation, and two broad categories of animals, arthropods and vertebrates. This update also adds the critical biological process, “Competition,” to capture the ways in which arthropods and vertebrates affect the rate of competition experienced by MNSW for habitat and food resources as larvae and adults. (Competition also covers the ways in which other plants compete with quailbush for water and space, discussed below). The link reason notes:

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(1) MNSW larvae may face competition for quailbush leaf resources—both for feeding and for building leaf shelters—from herbivorous vertebrates that may browse on quailbush foliage. (2) MNSW adults may face competition from herbivorous vertebrates that feed on the leaves or flowers of MNSW nectar sources (see table 3). For both larval and adult MNSW, changes in the arthropod assemblage would be expected to result in changes in the types and intensities of competition that the MNSW face. The link is hypothesized to be unidirectional and positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of vertebrates present, the greater the competition MNSW larvae or adults will face from vertebrates. The link is proposed to have unknown intensity and high spatial and temporal scales: The relationship has not been evaluated with field data, but the effects will be widespread and year round. Link predictability is unknown and link understanding low: The principles of the relationship are well understood in general, but the relationship has not been studied specifically in the LCR ecosystem. *Applies to Larvae and Adults.*

- Vertebrate Assemblage effects on Predation (CAP): As noted above, this update drops the habitat element, “Predators,” and replaces it with two broad categories of animals, “Arthropod Assemblage” and “Vertebrate Assemblage,” and recognizes that MNSW in all life stages can experience predation from both classes of animals. This update notes that insectivorous birds are known to prey on butterflies in all life stages, in general, and have been observed feeding on numerous Lepidoptera in the LCR ecosystem in particular (Anderson 2012), although not specifically on MNSW. These insectivorous birds include species that feed from the air and some that feed on the ground, including beneath the quailbush canopy (i.e., Gambel’s quail). Insectivorous small mammals, reptiles, and amphibians also occur in the LCR ecosystem. However, there are no published reports of either arthropods or vertebrates preying specifically on MNSW, in any life stage, apparently because the topic has not been studied. Nevertheless, changes in the vertebrate assemblage would be expected to result in changes in the types and intensities of predation that the MNSW face. The link is hypothesized to be positive, with no or an unknown threshold, on the assumption that the greater the diversity and abundance of vertebrates present, the greater the predation MNSW in all life stages will experience from vertebrates. The link is proposed to have unknown intensity and high spatial and temporal scales: The relationship has not been evaluated with field data, but the effects will be widespread and year round. The link has unknown link predictability and low understanding. *Applies to all life stages.*

- **Woody Vegetation Assemblage effects on Foraging (CAP):** The original CEM noted possible effects of MNSW nectar sources on adult feeding/watering (renamed “Foraging” in this update). As noted above, this update identifies two broad categories of plants, herbaceous and woody vegetation, and recategorizes nectar sources as components of either the herbaceous or woody vegetation assemblages. This update therefore addresses the effects of herbaceous and woody vegetation (see below) on adult foraging separately. The link reason notes that MNSW adults feed on nectar from a range of herbaceous and woody plants, as discussed in chapter 3, “Foraging,” and chapter 4, “Herbaceous Vegetation Assemblage” and “Woody Vegetation Assemblage.” The types, distribution, and condition of nectar sources available within the woody vegetation assemblage in and around MNSW sites, and their variation over time, therefore affect the amount of energy that MNSW adults must expend to obtain nectar, the distances and time they must fly to reach nectar sources, and the amount of sugar and other nutrients that they are able to obtain during feeding. The hypothesized link is proposed to be unidirectional and complex: The causal node and/or effect node include(s) several variables, and the effects of the former on the latter therefore are necessarily complex. The link is proposed to have high intensity, spatial scale, and temporal scale, with high predictability and high understanding. The link understanding reason notes: Relative to other topics concerning MNSW, this hypothesized relationship is comparatively well studied. Gaps in knowledge remain, however (e.g., how MNSW select among alternative potential nectar sources based on the food quality, availability, and spatial distribution of these sources and how far MNSW will travel in search of nectar during periods of scarcity). *Applies to Adults.*
- **Woody Vegetation Assemblage effects on Thermal Stress (CAP):** The original CEM (Braun 2015) addressed thermal stress under the broader category of physiological stress. This update separates physiological stress into two parts, mechanical and thermal stress. As noted above, this update categorizes the plants that may occur within and around quailbush patches as either herbaceous or woody vegetation. This update therefore addresses the effects of herbaceous (see above) and woody vegetation on thermal stress separately. As discussed above (see effects of quailbush patch size and structure effects on thermal stress), shading by vegetation provides a crucial buffer for MNSW eggs, larvae, pupae, and adults from stress from elevated air temperatures. As part of this larger relationship, MNSW may prefer quailbush patches that incorporate or lie adjacent to trees, the shade of which may provide some additional protection against the heat (J. Hill and C. Ronning 2018, joint personal communication; Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 1997). The hypothesized link is proposed to be unidirectional and complex because the cause and effect node both include several variables with complex interactions. It is proposed to have medium



intensity and high temporal scale, but unknown spatial scale because data and reports do not indicate how often and in what spatial relationships woody vegetation occurs in association with quailbush patches. MNSW eggs, larvae, and pupae have no means for changing their locations to take advantage of arboreal shade. Maternal ovipositing choices determine whether or not they benefit from any arboreal shade available in their natal patch. MNSW adults clearly use shade to help them avoid exposure to elevated air temperatures. Woody vegetation structure and proximity help determine the extent of opportunities for such shade for adults. The link has medium predictability based on the frequency with which the relationship has been observed, even if only anecdotally and medium understanding based on a small number of observations available. *Applies to all life stages.*

## **NEW LINKS WITH CRITICAL ACTIVITIES/ PROCESSES AS CAUSAL AGENTS**

- **Chemical Stress effects on Adult Fertility (LSO):** The original CEM included a link between “contamination and infection” and “physiological stress” but did not include a link from physiological stress to adult fertility (Braun 2015). As noted above, this update divides and replaces contamination and infection with chemical stress and disease, and replaces physiological stress with mechanical stress and thermal stress. Each of these four types of stress directly affects adult fertility in this update. As described in chapter 3 (see “Chemical Stress”), MNSW in all life stages are vulnerable to harm from anthropogenic contaminants or from natural substances at extreme concentrations. Direct contact with harmful chemicals can cause chemical stress that impairs adult fertility, as is known to happen in butterflies in general (Hoskins 2015; Scott 1986). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW adults, the greater the likelihood of impaired fertility. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Adults.*
- **Chemical Stress effects on Egg Growth (LSO):** Egg growth is a new life-stage outcome added to the CEM in this update. As described in chapter 3 (see “Chemical Stress”), MNSW in all life stages are vulnerable to harm from anthropogenic contaminants or from natural substances at extreme concentrations. Direct contact with harmful chemicals can cause chemical stress that impairs egg growth as is known to happen in butterflies in

general (Hoskins 2015; Scott 1986). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW eggs, the greater the likelihood of impaired egg growth. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Eggs.*

- **Chemical Stress effects on Larval Growth (LSO):** Larval growth is a new life-stage outcome added to the CEM in this update. As described in chapter 3 (see “Chemical Stress”), MNSW in all life stages are vulnerable to harm from anthropogenic contaminants or from natural substances at extreme concentrations. Direct contact with harmful chemicals can cause chemical stress that impairs larval growth, as is known to happen in butterflies in general (Hoskins 2015; Scott 1986). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW larvae, the greater the likelihood of impaired larval growth. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Larvae.*
- **Competition effects on Foraging (CAP):** MNSW larvae theoretically experience competition for leaf nutrition from other MNSW larvae and potentially from the larvae of saltbush sootywing and western pygmy blue butterflies (see chapter 4, “Arthropod Assemblage”). Other possible competitors with MNSW larvae for quailbush leaf nutrition include insects such as ensign coccids, aphids, grasshoppers, cicadas, and a moth (*Trichocosmia inornata*); and herbivorous mammals (see chapter 4, “Arthropod Assemblage” and “Vertebrate Assemblage”). In turn, MNSW adults theoretically experience competition for nectar resources from a wide range of Lepidoptera (see chapter 4, “Arthropod Assemblage”) as well as from an unknown range of animals that may feed on the nectar, flowers, or leaves of the same plants (see chapter 4, “Arthropod Assemblage” and “Vertebrate Assemblage”). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the competition that MNSW larvae or adults experience in their foraging efforts, the less successful they will be in these foraging efforts. The link is proposed to have low intensity and high spatial and temporal scales: The literature reviewed for this CEM identifies an array of possible competitors that are likely widely distributed and active throughout the same times of the year as are MNSW. However, the literature does not suggest that MNSW larvae or adults forage less successfully as a result of competition. Link

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predictability is unknown and link understanding low: The relationship is theoretically plausible but has not been formally studied. *Applies to Larvae and Adults.*

- Competition effects on Resting/Hiding (CAP): Theoretically, the same species that may compete with MNSW larvae for foraging resources may also compete for resting/hiding habitat by occupying or consuming leaves that provide the best resting/hiding habitat. In turn, theoretically, these same species may also limit opportunities for resting/hiding by MNSW adults within quailbush shrub canopy. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the competition that MNSW larvae or adults experience in their efforts to find suitable resting/hiding habitat within quailbush shrubs, the less successful they will be in these search efforts. The link is proposed to have low intensity and high spatial and temporal scales: The literature reviewed for the CEM identifies an array of possible competitors that are likely widely distributed and active throughout the same times of the year as are MNSW. However, the literature does not suggest that MNSW larvae or adults are less successful at finding suitable resting/hiding habitat as a result of competition. Link predictability is unknown and link understanding low: The relationship is theoretically plausible but has not been formally studied. *Applies to Larvae and Adults.*
- Disease effects on Egg Growth (LSO): The original CEM included a link between “contamination and infection” and “physiological stress” but did not include a link from physiological stress to adult fertility (Braun 2015). As noted above, this update divides and replaces contamination and infection with chemical stress and disease, and replaces physiological stress with mechanical stress and thermal stress. Each of these four types of stress directly affects egg growth in this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction. However, the literature reviewed for the CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among eggs, and consequently no information on the impacts of disease on egg growth. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW eggs, the greater the likelihood of impaired growth. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Eggs.*

## Updates to Chapter 6 – Conceptual Ecological Model by Life Stage

- Disease effects on Larval Growth (LSO): The original CEM included a link between “contamination and infection” and “physiological stress” but did not include a link from physiological stress to adult fertility (Braun 2015). As noted above, this update divides and replaces contamination and infection with chemical stress and disease, and replaces physiological stress with mechanical stress and thermal stress. Each of these four types of stress directly affects larval growth in this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction. However, the literature reviewed for this CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among larvae, and consequently no information on the impacts of disease on larval growth. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW eggs, the greater the likelihood of impaired growth. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Larvae.*
- Foraging effects on Adult Fertility (LSO): As noted in the discussion of ovipositing and the effects of foraging success on ovipositing, MNSW females prior to ovipositing ingest significant quantities of nectar, preferentially selecting flowers with higher nectar sugar content and spending more time feeding when flowers have lower sugar content (Wiesenborn 2010b, 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 2010b, 2011; Wiesenborn and Pratt 2010). MNSW adult females—like other butterflies described in the literature—may prefer nectar with higher concentrations of amino acids (Boggs 2003; Nelson et al. 2015; Pratt and Wiesenborn 2009; Rosa et al. 2017; Vande Velde et al. 2013; Wiesenborn 2010b; Wiesenborn and Pratt 2010). 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 foraging success must be crucial to ovipositing success because females need such high nutritional inputs for only one purpose: ovipositing. In turn, the general literature on herbivorous insects suggests that foraging success also should affect fecundity and fertility (Awmack and Leather 2002). However, the literature reviewed for this CEM provides no information on this possible

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relationship specifically for MNSW or any related butterflies. The hypothesized link is proposed to be unidirectional and positive, with no threshold, on the assumption that greater foraging success should result in greater fertility. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low: The relationship is theoretically plausible but has not been studied in MNSW anywhere. *Applies to Adults.*

- Foraging effects on Larval Growth (LSO): Studies across a wide range of butterfly species suggest that impaired diets among larvae affect larval growth rates, duration, and resulting adult morphology, foraging and mating behavior, fecundity, and physiology and development in subsequent generations (Awmack and Leather 2002; Boggs 2003; Boggs and Niitepõld 2014; Gibbs et al. 2012, 2018; Johnson et al. 2014; Rosa and Saastamoinen 2017; Saastamoinen et al. 2013; Vande Velde et al. 2013; Woestmann and Saastamoinen 2016). These relationships have been observed across numerous butterfly species (see review by Woestmann and Saastamoinen 2016) but have not been studied in any species closely related to MNSW, let alone specifically in MNSW. The hypothesized link is proposed to be unidirectional and positive, with no threshold, on the assumption that greater foraging success should result in greater larval growth and vice versa. The link is proposed to have medium intensity and high spatial and temporal scales: The relationship is theoretically plausible and documented in other butterfly species but has not been studied specifically in MNSW. Link predictability therefore is unknown and link understanding low: The relationship is theoretically plausible but has not been studied in MNSW anywhere. *Applies to Larvae.*
- Mechanical Stress effects on Adult Fertility (LSO): The original CEM included “Physiological Stress” as a critical biological process but did not include a link from “Physiological Stress” to “Adult Fertility” (Braun 2015). As noted above, this update replaces physiological stress with mechanical stress and thermal stress, both of which directly affect adult fertility in this update. As described in chapter 3 (see “Mechanical Stress”), MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to harmful winds or intense precipitation, physical disturbance of individual quailbush shrubs, and capture and handling for study. Such stress is hypothesized as a potential cause of impaired fertility. However, the literature reviewed for this CEM indicates that MNSW adults have the ability to fly away from potentially mechanically stressful conditions, including hiding in quailbush foliage and flying close to the ground to escape or avoid strong winds. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of mechanical stress

among adults, the lower their fertility. The link is proposed to have low intensity and high spatial and temporal scales. Link predictability is unknown and link understanding low. *Applies to Adults.*

- **Mechanical Stress effects on Larval Growth (LSO):** Larval growth is a new life-stage outcome added to the CEM in this update. As described in chapter 3 (see “Mechanical Stress”), MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to harmful winds or intense precipitation, physical disturbance of individual quailbush shrubs, and capture and handling for study. Unavoidable or inescapable mechanical stress to MNSW larvae presumably may kill or weaken individual MNSW or disrupt growth and development. MNSW larval use of leaf shelters, in turn, presumably helps protect the larvae from sources of mechanical stress, such as harmful winds, intense precipitation, and other physical disturbance of individual quailbush shrubs, such as by passing animals. However, the literature reviewed for this CEM provides no specific information on the relationship. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that greater mechanical stress should result in impaired larval growth. The link is proposed to have low intensity and high spatial and temporal scales: The relationship is theoretically plausible but has not been studied specifically in MNSW, and MNSW larvae have some ability to shelter themselves from common sources of mechanical stress. Link predictability is unknown and link understanding low: The relationship is theoretically plausible but has not been studied in MNSW. *Applies to Larvae.*
- **Thermal Stress effects on Adult Fertility (LSO):** The original CEM included “physiological stress” as a critical biological process but did not include a link from physiological stress to reproductive output (Braun 2015). This update replaces reproductive output with fertility and replaces physiological stress with mechanical stress and thermal stress, both of which directly affect fertility in this update. MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Unavoidable or inescapable thermal stresses are hypothesized as a potential cause of impaired fertility. However, the literature reviewed for this CEM indicates that MNSW adults use several strategies to reduce or cope with their exposure to extreme temperatures (see chapter 3, Resting/Hiding”). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among adults, the lower their fertility. The link is proposed to have low intensity and unknown spatial and temporal scales: The relationship is plausible but unstudied, and the spatial and temporal distributions of temperatures sufficient to inhibit fertility are unknown. Link predictability is unknown and link understanding low. *Applies to Adults.*

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- Thermal Stress effects on Egg Growth (LSO): The original CEM did not include egg growth as a life-stage outcome and included “physiological stress” as a critical biological process (Braun 2015). This update adds egg growth as a life-stage outcome and replaces physiological stress with mechanical stress and thermal stress, both of which directly affect egg growth in this update. MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Exposure to temperature extremes is a known cause of altered egg development in butterflies (Woestmann and Saastamoinen 2016). Further, MNSW appear to have evolved ovipositing behaviors that result in the placement of eggs in locations on quailbush shrubs and particular types of locations within these shrubs that would have the effect of buffering the eggs from temperature extremes (see effects of thermal stress on ovipositing in the updates to chapter 3). However, no studies of MNSW eggs and hatching reviewed for this CEM (e.g., Wiesenborn 2012a) specifically discuss the possible effects of extreme temperatures on MNSW egg hatching or rates of hatching success. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among eggs, the greater the likelihood of altered growth and development. The link is proposed to have low intensity, high spatial scale, and unknown temporal scale: The relationship is plausible, and MNSW appear to have evolved ovipositing behaviors that result in the placement of eggs in locations on quailbush shrubs (e.g., with a balance of shade) that are less vulnerable to thermal stress, but the relationship is unstudied for MNSW, and the temporal distributions of extreme temperatures outside the normal range of variation is unknown. Link predictability is unknown and link understanding medium. *Applies to Eggs.*
- Thermal Stress effects on Larval Growth (LSO): The original CEM did not include larval growth as a life-stage outcome and included “physiological stress” as a critical biological process (Braun 2015). This update adds larval growth as a life-stage outcome and replaces physiological stress with mechanical stress and thermal stress, both of which directly affect larval growth in this update. MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Exposure to temperature extremes is a known cause of altered larval development in butterflies (Woestmann and Saastamoinen 2016). However, MNSW larvae build and spend most of each day inside a leaf shelter that is assumed to provide some protection from thermal stress (see chapter 3, “Resting/Hiding”). Further, MNSW ovipositing behavior appears adapted to placing eggs on particular quailbush shrubs and particular types of locations within these shrubs that would have the effect of buffering the eggs from temperature extremes (see effects of thermal stress on ovipositing in the updates to chapter 3). To the extent that MNSW larvae

complete this life stage without moving far beyond their natal locations, the effects of such ovipositing behaviors should be to buffer MNSW larvae from the effects of extreme temperature as well. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among larvae, the greater the likelihood of altered growth and development. The link is proposed to have low intensity, high spatial scale, and unknown temporal scale: The relationship is plausible, and MNSW appear to have evolved ovipositing and larval behaviors that result in the larvae being protected from thermal stress not only by their leaf shelters but by their locations on quailbush shrubs and the locations of the shrubs in relation to shading trees. However, the relationship has not been systematically studied for MNSW, and the temporal distribution of extreme temperatures outside the normal range of variation is unknown. Link predictability is unknown and link understanding medium. *Applies to Larvae.*

## DELETED LINKS WITH CRITICAL ACTIVITIES/ PROCESSES AS CAUSAL AGENTS

- Effects of Contamination and Infection on Physiological Stress. This update replaces “Contamination and Infection” with two separate critical biological processes, “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to all life stages.*
- Effects of Feeding/Watering on Physiological Stress. This update replaces “Feeding/Watering” with “Foraging” and replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to Larvae and Adults.*
- Effects of Hiding/Resting on Physiological Stress. This update replaces “Hiding/Resting” with “Resting/Hiding” and replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal stress.” *Applies to Larvae, Pupae, and Adults.*
- Effects of Physiological Stress on Ovipositing. This update replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to Adults.*
- Effects of Physiological Stress on Adult Survival. This update replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to Adults.*



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- Effects of Physiological Stress on Egg Survival. This update replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to Eggs.*
- Effects of Physiological Stress on Larval Survival. This update replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to Larvae.*
- Effects of Physiological Stress on Pupal Survival. This update replaces “Physiological Stress” with two separate biological processes, “Mechanical Stress” and “Thermal Stress.” *Applies to Pupae.*
- Effects of Predation on Reproductive Output Rate. This update replaces the link from “Predation” to “Adult Fertility” (formerly “Reproductive Output Rate”) with a link from “Adult Survival” to “Adult Fertility.”
- Effects of Predation on Adult Dispersal Rate. This update replaces the link from “Predation” to “Adult Dispersal” with a link from “Adult Survival” to “Adult Dispersal.”

## **UPDATED LINKS WITH CRITICAL ACTIVITIES/ PROCESSES AS CAUSAL AGENTS**

- Chemical Stress effects on Adult Survival (LSO): The original CEM included a link between “Contamination and Infection” and “Physiological Stress,” and a link from “Physiological Stress” to “Adult Survival” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects adult survival in this update. MNSW adults suffering from chemical stress presumably experience lower rates of survival through directly fatal reactions or through impaired abilities to avoid predation, avoid conditions that could result in mechanical stress or thermal stress, or fight off disease. However, while theoretically plausible for MNSW, the literature reviewed for this CEM does not address the topic. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW adults, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to adults.*

- Chemical Stress effects on Egg Survival (LSO): The original CEM included a link between “Contamination and Infection” and “Physiological Stress,” and a link from “Physiological Stress” to “Adult Survival” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects egg survival in this update. MNSW eggs suffering from chemical stress presumably experience lower rates of survival through directly fatal reactions, in addition to impaired growth (see above). However, while theoretically plausible for MNSW, the literature reviewed for this CEM does not address the topic. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW eggs, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to eggs.*
- Chemical Stress effects on Larval Survival (LSO): The original CEM included a link between “Contamination and Infection” and “Physiological Stress,” and a link from “Physiological Stress” to “Adult Survival” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects egg survival in this update. MNSW larvae suffering from chemical stress presumably experience lower rates of survival through directly fatal reactions or through impaired abilities to avoid predation, avoid conditions that could result in mechanical stress or thermal stress, or fight off disease. However, while theoretically plausible for MNSW, the literature reviewed for this CEM does not address the topic. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW larvae, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to larvae.*
- Chemical Stress Effects on Ovipositing (CAP): The original CEM included a link between “Contamination and Infection” and “Physiological Stress,” and a link from “Physiological Stress” to “Ovipositing” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces

“Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects ovipositing in this update. MNSW adult females suffering from chemical stress presumably experience lower rates of successful ovipositing, in addition to presumably also experiencing lower survival and fertility (see above). However, while theoretically plausible for MNSW, the literature reviewed for this CEM does not address the topic. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW adult females, the greater the likelihood of impaired ovipositing. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Adults.*

- **Chemical Stress Effects on Pupal Survival (LSO):** The original CEM included a link between “Contamination and Infection” and “Physiological Stress,” and a link from “Physiological Stress” to “Adult Survival” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects egg survival in this update. MNSW pupae suffering from chemical stress presumably experience lower rates of survival through directly fatal reactions or reactions that impair maturation, leading to death. However, while theoretically plausible for MNSW, the literature reviewed for this CEM does not address the topic. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of chemical stress to MNSW pupae, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Pupae.*
- **Disease Effects on Adult Fertility (LSO):** The original CEM included a link between “Contamination and Infection” and “Physiological Stress” but did not include a link from “Physiological Stress” to “Adult Fertility” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects adult fertility in this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual

insects, or disrupt growth, development, or reproduction. However, the literature reviewed for this CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among adults, and consequently no information on the impacts of disease on adult fertility. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW adults, the greater the likelihood of impaired fertility. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Adults.*

- Disease Effects on Adult Survival (LSO): The original CEM included a link between “Contamination and Infection” and “Physiological Stress” but did not include a link from “Physiological Stress” to “Adult Fertility” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects adult survival in this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction. However, the literature reviewed for this CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among adults, and consequently no information on the impacts of disease on adult survival. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW adults, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Adults.*
- Disease effects on Egg Survival (LSO): The original CEM included a link between “Contamination and Infection” and “Physiological Stress” but did not include a link from “Physiological Stress” to “Adult Fertility” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects egg survival in this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi,

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and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction. However, the literature reviewed for this CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among eggs, and consequently no information on the impacts of disease on egg survival. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW eggs, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Eggs.*

- **Disease Effects on Larval Survival (LSO):** The original CEM included a link between “Contamination and Infection” and “Physiological Stress” but did not include a link from “Physiological Stress” to “Adult Fertility” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects larval survival in this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction. However, the literature reviewed for this CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among larvae, and consequently no information on the impacts of disease on larval survival. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW larvae, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Larvae.*
- **Disease Effects on Pupal Survival (LSO):** The original CEM included a link between “Contamination and Infection” and “Physiological Stress” but did not include a link from “Physiological Stress” to “Adult Fertility” (Braun 2015). As noted above, this update divides and replaces “Contamination and Infection” with “Chemical Stress” and “Disease,” and replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress.” Each of these four types of stress directly affects pupal survival in

this update. As described in chapter 3 (see “Disease”), MNSW in all life stages theoretically are vulnerable to infection by viruses, bacteria, fungi, and parasites, as is the case for all butterflies (Altizer and de Roode 2010; Scott 1986). Infections may kill or weaken individual insects, or disrupt growth, development, or reproduction. However, the literature reviewed for this CEM provides no information on the types or incidences of disease among MNSW in any life stage, let alone specifically among pupae, and consequently no information on the impacts of disease on pupal survival. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the frequency and intensity of disease among MNSW pupae, the greater the likelihood of impaired survival. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is theoretically plausible but has not been studied in MNSW anywhere. Link predictability therefore is unknown and link understanding low. *Applies to Pupae.*

- **Mechanical Stress Effects on Adult Survival (LSO):** The original CEM included “Physiological Stress” as a critical biological process and included a link from “Physiological Stress” to “Adult Survival” (Braun 2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect adult survival in this update. As described in chapter 3 (see “Mechanical Stress”), MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to harmful winds, intense precipitation, physical disturbance of individual quailbush shrubs, and capture and handling for study. Unavoidable or inescapable mechanical stress to MNSW adults presumably may directly kill individual MNSW adults, or weaken the stressed individuals, reducing their ability to respond to other threats. However, the literature reviewed for this CEM indicates that MNSW adults have the ability to fly away from potentially mechanically stressful conditions, including hiding in quailbush foliage and flying close to the ground to escape or avoid strong winds. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of mechanical stress among adults, the lower their rate of survival. The link is proposed to have low intensity and high spatial and temporal scales. Link predictability is unknown and link understanding low. *Applies to Adults.*
- **Mechanical Stress Effects on Larval Survival (LSO):** The original CEM included “Physiological Stress” as a critical biological process and included a link from “Physiological Stress” to “Larval Survival” (Braun 2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect larval survival in this update. As described in chapter 3 (see “Mechanical

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Stress”), MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to harmful winds, intense precipitation, physical disturbance of individual quailbush shrubs, and capture and handling for study. Unavoidable or inescapable mechanical stress to MNSW larvae presumably may kill or weaken individual MNSW, leaving them more vulnerable to other threats. MNSW larval use of leaf shelters, in turn, presumably helps protect the larvae from sources of mechanical stress, such as harmful winds, intense precipitation, and other physical disturbance of individual quailbush shrubs, such as by passing animals. However, the literature reviewed for this CEM provides no specific information on the relationship. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that greater mechanical stress should result in impaired larval survival. The link is proposed to have low intensity and high spatial and temporal scales: The relationship is theoretically plausible, but has not been studied specifically in MNSW, and MNSW larvae have some ability to shelter themselves from common sources of mechanical stress. Link predictability is unknown and link understanding low: The relationship is theoretically plausible but has not been studied in MNSW. *Applies to Larvae.*

- **Mechanical Stress Effects on Ovipositing (CAP):** The original CEM included “Physiological Stress” as a critical biological process and included a link from “Physiological Stress” to “Ovipositing” (Braun 2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect ovipositing in this update. As described in chapter 2 (see “Mechanical Stress”), MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to harmful winds, intense precipitation, physical disturbance of individual quailbush shrubs, and capture and handling for study. Mechanically potentially stressful conditions such as strong winds or disturbance of quailbush foliage presumably can directly disrupt ovipositing, and repeated or persistent disturbances presumably would be more harmful than single events. However, the literature reviewed for this CEM does not address this topic. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the incidence of potentially mechanically stressful conditions, the greater the likelihood of disruption to ovipositing. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is plausible but unstudied. Link predictability is unknown and link understanding low. *Applies to Adults.*
- **Mechanical Stress Effects on Pupal Survival (LSO):** The original CEM included “Physiological Stress” as a critical biological process and included a link from “Physiological Stress” to “Pupal Survival” (Braun

2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect pupal survival in this update. As described in chapter 3 (see “Mechanical Stress”), MNSW in every life stage are vulnerable to mechanical stress resulting from inundation, wildfire, exposure to harmful winds, intense precipitation, physical disturbance of individual quailbush shrubs, and capture and handling for study. Otherwise, the literature reviewed for this CEM provides no specific information on the relationship. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that greater mechanical stress should result in impaired pupal survival. The link is proposed to have low intensity and high spatial and temporal scales: The relationship is theoretically plausible, but has not been studied specifically in MNSW, and MNSW pupae benefit from the ability of their larvae to shelter themselves from common sources of mechanical stress. Link predictability is unknown and link understanding low: The relationship is theoretically plausible but has not been studied in MNSW. *Applies to Pupae.*

- Resting/Hiding Effects on Mechanical Stress (CAP): As noted above, the original CEM included “Physiological Stress,” which this update replaces with “Mechanical Stress” and “Thermal Stress.” Unavoidable or inescapable mechanical stress to MNSW larvae presumably may directly kill individual MNSW larvae, or weaken the stressed individuals, reducing their ability to respond to other threats. However, as also noted above, MNSW larvae build and live in leaf shelters that provide some safety from mechanical stress. On the other hand, such behaviors provide no safety from disturbances that may affect entire quailbush shrubs or patches such as inundation, wildfire, or physical disturbance of quailbush shrubs by large animals or machinery. As noted above, in turn, pupae cannot move to avoid or escape mechanical stress. However, MNSW pupate in their final larval leaf shelters, which affords some passive protection that may also vary with the location of the pupation site within the individual quailbush shrub. Similarly, unavoidable or inescapable mechanical stress to MNSW adults presumably may directly kill individual MNSW adults, or weaken the stressed individuals, reducing their ability to respond to other threats. However, as also noted above, MNSW adults routinely avoid and escape potentially mechanically stressful winds by hiding in quailbush foliage (Nelson et al. 2014, 2015; Pratt and Wiesenborn 2011) and possibly in the foliage of other woody vegetation as well (Wiesenborn 1997). On the other hand, such behaviors provide no safety from other kinds of disturbance such as wildfire or physical disturbance of quailbush shrubs by large animals or machinery. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that MNSW larval or adult success in maintaining or finding safe resting/hiding habitat to avoid mechanically stressful conditions, and larval



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pupation in leaf shelters, will lower the rate of mechanical stress the MNSW experience. The link is proposed to have medium intensity and high spatial and temporal scales. Link predictability and link understanding are medium. *Applies to Larvae, Pupae, and Adults.*

- Resting/Hiding Effects on Monitoring, Capture, Handling (HE): As noted above, Ronning (2018) provides information on ways in which MNSW adult basking and perching behavior may affect the detectability of basking and perching MNSW adults. The link reason therefore is updated with the addition of the following: Ronning (2018, personal communication) also notes that MNSW adults are “very still” when basking or perching, and this stillness makes it more difficult to detect them during field investigations. “They can be hard to detect due to their small size and the mottled shade of the shrubs even when perched on the outside of a quailbush until they start flying again. That stillness would have made it hard to detect one I saw basking on the ground if I hadn’t been following it at the time.” All other information for this link remains unchanged. *Applies only to Adults.*
- Resting/Hiding Effects on Predation (CAP): As noted above, Ronning (2018) provides information on ways in which MNSW adult basking and perching behavior may affect the detectability of basking and perching MNSW adults. The link reason therefore is updated as follows: MNSW adults stay almost exclusively within the cover of quailbush shrub canopies when they are not traveling to or searching for nectar sources. Theoretically, adult MNSW within quailbush canopy would be less visible to predators such as insectivorous birds and flying insects overhead. Ronning (2018, personal communication) also notes that MNSW adults are “very still” when basking or perching, and this stillness makes it more difficult to detect them during field investigations (see effects of resting/hiding on monitoring in the updates to chapter 3). As a corollary, one may hypothesize that the stillness could also affect the detectability of basking or perching MNSW by predators scanning quailbush external surfaces. However, the literature reviewed for this CEM provides no specific information on potential predators on MNSW of any life stage (see chapter 3, “Predation,” and chapter 4, “Predators”) nor on ways in which MNSW resting/hiding behaviors may affect rates of predation. Wiesenborn (2010) notes this lack of information on predation (and parasitism) as a significant gap in knowledge of the species. All other information for this link remain unchanged. *Applies only to Adults.*
- Resting/Hiding Effects on Thermal Stress (CAP): As noted above, the original CEM included “physiological stress” as a critical biological process, and included links from hiding/resting to physiological stress. This update replaces physiological stress with mechanical stress and thermal stress. MNSW in every life stage are vulnerable to thermal stress

resulting from exposure to air temperatures above or below their limits of tolerance. Unavoidable or inescapable thermal stresses may kill or weaken individual MNSW, or disrupt growth, development, or reproduction. However, as discussed in chapter 3 (see “Resting/Hiding”), MNSW larvae and adults display a range of behaviors for avoiding or escaping potentially thermally stressful conditions. These behaviors include the larval use of leaf shelters and possibly the placement of these shelters within the quailbush foliage. Pupae, of course, cannot move to avoid or escape thermal stress. However, MNSW pupate in their final larval leaf shelters, which affords some passive protection from thermal stress, which may also vary with the location of the pupation site within the individual quailbush shrub. Adult MNSW use the shade of quailbush foliage and of trees that may overshadow quailbush shrubs to avoid thermal stress, greatly reduce their activity during the hottest hours of the day, and rest with wings closed, which is a common means of thermal regulation in butterflies (Nelson et al. 2014; Pratt and Wiesenborn 2011; Wiesenborn 1997, 1999, 2010). MNSW adults also exhibit specific resting behaviors in response to excessively low temperatures: In contrast to their behavior during hotter days and hours, MNSW adults bask in sunlight during cooler days and hours of the day with their wings open presumably to raise their body and wing temperatures for flight (Pratt and Wiesenborn 2009). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that MNSW larval or adult success in maintaining or finding safe resting/hiding habitat and body postures to avoid thermally stressful conditions, and larval pupation in leaf shelters, will lower the rate of thermal stress the MNSW experience. The link is proposed to have medium intensity and high spatial and temporal scales. Link predictability is medium and link understanding high for adults, but both are low for larvae and pupae: The detailed information available on how MNSW cope with air temperature extremes only concerns MNSW adults. The literature reviewed for this CEM provides no observational information on whether or how MNSW larvae or pupae may be affected (stressed) by temperature extremes. *Applies to Larvae, Pupae, and Adults.*

- **Thermal Stress Effects on Adult Survival (LSO):** The original CEM included “Physiological Stress” as a critical biological process and included a link from “Physiological Stress” to “Adult Survival” (Braun 2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect adult survival. As described in chapter 3 (see “Thermal Stress”), MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Unavoidable or inescapable thermal stresses may kill MNSW adults or weaken them, reducing their ability to respond to other threats. However, the literature reviewed for this CEM indicates that MNSW adults use several strategies

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to reduce or cope with their exposure to extreme temperatures (see chapter 3, “Resting/Hiding”). The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among adults, the lower their chances of survival. The link is proposed to have high intensity and spatial scale but unknown temporal scale: The relationship is biologically plausible and moderately well documented, but not systematically studied in MNSW, and likely applies throughout the LCR ecosystem. However, while the seasonal distribution of high temperatures is stable, the incidence of extreme temperatures outside the normal range of variation is unknown. Link predictability and link understanding appear to be medium. *Applies to adults.*

- **Thermal Stress Effects on Egg Survival (LSO):** The original CEM included “physiological stress” as a critical biological process (Braun 2015) affecting egg survival. The CEM replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect egg survival in this update. MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Exposure to temperature extremes is a known cause of butterfly egg mortality (Radchuk et al. 2013). Further, MNSW ovipositing behavior appears adapted to placing eggs on particular quailbush shrubs and particular types of locations within these shrubs that would have the effect of buffering the eggs from temperature extremes (see effects of thermal stress on ovipositing in the updates to chapter 3). However, no studies of MNSW eggs and hatching reviewed for this CEM (e.g., Wiesenborn 2012a) specifically discuss the possible effects of extreme temperatures on MNSW egg hatching or rates of hatching success. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among eggs, the lower their rate of survival. The link is proposed to have low intensity, high spatial scale, and unknown temporal scale: The relationship is plausible, and MNSW appear to have evolved ovipositing behaviors that result in the placement of eggs in locations on quailbush shrubs (e.g., with a balance of shade) that are less vulnerable to thermal stress, but the relationship is unstudied for MNSW, and the temporal distributions of extreme temperatures outside the normal range of variation is unknown. Link predictability is unknown and link understanding medium. *Applies to eggs.*
- **Thermal Stress Effects on Larval Survival (LSO):** The original CEM included “Physiological Stress” as a critical biological process affecting larval survival (Braun 2015). This update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect larval survival in this update. MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures

above or below their limits of tolerance. Exposure to temperature extremes is a known cause of altered larval survival in butterflies (Radchuk et al. 2013). However, MNSW larvae build and spend most of each day inside a leaf shelter that is thought to provide some protection from thermal stress (see chapter 3, “Resting/Hiding”). Further, MNSW ovipositing behavior appears adapted to placing eggs on particular quailbush shrubs and particular types of locations within these shrubs that would have the effect of buffering the eggs from temperature extremes (see effects of thermal stress on ovipositing in the updates to chapter 3). To the extent that MNSW larvae complete this life stage without moving far beyond their natal locations, the effects of such ovipositing behaviors should be to buffer MNSW larvae from the effects of extreme temperature as well. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among larvae, the lower their survival. The link is proposed to have low intensity, high spatial scale, and unknown temporal scale: The relationship is plausible, and MNSW appear to have evolved ovipositing and larval behaviors that result in the larvae being protected from thermal stress not only by their leaf shelters but by their locations on quailbush shrubs and the locations of the shrubs in relation to shading trees. However, the relationship has not been systematically studied for MNSW, and the temporal distribution of extreme temperatures outside the normal range of variation is unknown. Link predictability is unknown and link understanding medium. *Applies to Larvae.*

- **Thermal Stress Effects on Ovipositing (CAP):** The original CEM included “Physiological Stress” as a critical biological process and included a link from “Physiological Stress” to “Ovipositing” (Braun 2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect ovipositing in this update. MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Unavoidable or inescapable thermal stresses may kill or weaken individual MNSW, or disrupt growth, development, or reproduction. This relationship holds for the effects of extreme temperatures on ovipositing as well. 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 skipper control its body temperature (Wiesenborn 1999). MNSW females appear to lay their eggs preferentially on quailbush growing in the shade of trees, another possible indication that shading matters in plant selection for ovipositing (Pratt and Wiesenborn (2011). Limited data also suggest that MNSW females oviposit more frequently during the morning and early afternoon (e.g., 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. This temporal pattern is consistent with the overall pattern of MNSW adults resting within the quailbush canopy during the hottest hours of the day and

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for longer periods on days with extremely high temperatures, and moving less at both high and low temperatures in general (Nelson et al. 2014, 2015; Pratt and Wiesenborn 2009; Wiesenborn 1999). Ovipositing on the undersides of leaves (Nelson et al. 2015; Pratt and Wiesenborn 2011) also shade MNSW eggs. The hypothesized link is proposed to be unidirectional and complex: Time spent ovipositing will be less on days with longer periods of extremely high temperatures, but MNSW females also may select ovipositing sites to minimize risks of thermal stress. The link is proposed to have high intensity and spatial scale but unknown temporal scale: The relationship is biologically plausible and moderately well documented, but not systematically studied in MNSW, and likely applies throughout the LCR ecosystem. However, while the seasonal distribution of high temperatures is stable, the incidence of extreme temperatures outside the normal range of variation is unknown. Link predictability and link understanding appear to be medium. *Applies to Adults.*

- **Thermal Stress Effects on Pupal Survival (LSO):** The original CEM included “Physiological Stress” as a critical biological process affecting pupal survival (Braun 2015). As noted above, this update replaces “Physiological Stress” with “Mechanical Stress” and “Thermal Stress,” both of which directly affect pupal survival in this update. As described in chapter 3 (see “Thermal Stress”), MNSW in every life stage are vulnerable to thermal stress resulting from exposure to air temperatures above or below their limits of tolerance. Exposure to temperature extremes is a known cause of altered pupal survival in butterflies (Radchuk et al. 2013). However, MNSW larvae pupate in a leaf shelter that they build and in which they spend most of each day, and this shelter is thought to provide some protection from thermal stress (see chapter 3, “Resting/Hiding”). Further, MNSW ovipositing behavior appears adapted to placing eggs on particular quailbush shrubs and particular types of locations within these shrubs that would have the effect of buffering the eggs from temperature extremes (see effects of thermal stress on ovipositing in the updates to chapter 3). To the extent that MNSW larvae complete this life stage and pupate without having moved far beyond their natal locations, the effects of such ovipositing behaviors should be to buffer MNSW pupae from the effects of extreme temperature as well. The hypothesized link is proposed to be unidirectional and negative, with no threshold, on the assumption that the greater the rates of thermal stress among pupae, the lower their survival. The link is proposed to have low intensity, high spatial scale, and unknown temporal scale: The relationship is plausible, and MNSW appear to have evolved ovipositing and larval behaviors that result in the pupae being protected from thermal stress not only by their leaf shelters but by their locations on quailbush shrubs and the locations of the shrubs in relation to shading trees. However, the relationship has not been systematically studied for MNSW, and the temporal distribution of

extreme temperatures outside the normal range of variation is unknown. Link predictability is unknown and link understanding medium. *Applies to Pupae.*

## NEW LINKS WITH LIFE-STAGE OUTCOMES AS CAUSAL AGENTS

- **Adult Survival Effects on Adult Dispersal (LSO):** The original CEM (Braun 2015) proposed that predation could affect adult dispersal by reducing adult survival. This update continues to recognize that predation affects adult survival, while removing the link from predation to adult dispersal and replacing it with a link from adult survival to adult dispersal. The rate of MNSW adult dispersal, measured as the number of adults that successfully disperse to quailbush patches other than their natal patch, necessarily will vary with the abundance of MNSW adults in their natal patches and their rates of survival. The hypothesized link is proposed to be unidirectional and positive, with no threshold, on the assumption that the greater the rates of MNSW adult survival, the greater the potential for dispersal. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is biologically plausible, but the literature provides no information on what factors may trigger MNSW dispersal, other than possibly rainfall, and no information on how adult survival affects dispersal. Link predictability is unknown and link understanding low. *Applies to adults.*
- **Adult Survival Effects on Adult Fertility (LSO):** The original CEM (Braun 2015) proposed that predation could affect adult fertility by removing adults from the pool of individuals that can attempt and survive mating and, subsequently, ovipositing. This update continues to recognize that predation affects adult survival, while removing the link from predation to adult fertility and replacing it with a link from adult survival to adult fertility. The rate of MNSW adult fertility necessarily will vary with the number of individuals present to attempt and survive mating and, subsequently, ovipositing. The hypothesized link is proposed to be unidirectional and positive, with no threshold, on the assumption that the greater the rates of MNSW adult survival, the greater the fertility rate. The link is proposed to have unknown intensity and spatial and temporal scales: The relationship is biologically plausible, but the literature provides no information on how adult survival may affect fertility. Link predictability is unknown and link understanding low. *Applies to Adults.*

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- Egg Growth Effects on Egg Survival (LSO): The original CEM (Braun 2015) did not include egg growth as a life-stage outcome. Egg growth necessarily affects egg survival. Eggs that hatch sooner are vulnerable for a shorter time to potentially lethal threats during that life stage. The hypothesized link is proposed to be unidirectional and positive, with no threshold, on the assumption that the greater the rate of MNSW egg growth, the greater their survival. The link is proposed to have high intensity and spatial and temporal scales: The relationship is biologically highly plausible, but the literature provides no information on how precisely MNSW egg growth may affect survival. Link predictability is unknown and link understanding low. *Applies to Eggs.*
- Larval Growth Effects on Larval Survival (LSO): The original CEM (Braun 2015) did not include larval growth as a life-stage outcome. Larval growth necessarily affects larval survival. Larvae that mature more quickly are vulnerable for a shorter time to potentially lethal threats during that life stage. On the other hand, larvae that aestivate—undergo extended diapause—during seasonal periods of drought may exhibit higher rates of survival. Nelson et al. (2015) note, “Variation in precipitation as it affects host plant growth influences diapause in butterflies... Extended diapause that occurs in late instar larvae or pupae is often observed in Lepidoptera that live in areas of seasonal drought ... Diapause is often broken after rains that provide moisture and encourage host plant growth ... Some skippers found in areas with low and unpredictable rainfall aestivate for months as late instar larvae, with the adult flight season highly responsive to rainfall episodes... MacNeill’s sootywings may have similar strategies and responses to rainfall events along the LCR.” Aestivating butterfly larvae exhibit no growth, with greatly slowed metabolism and breathing (Scott 1986). If seasonal drought is the main trigger of larval aestivation, MNSW larvae will experience such seasonal drought through their sensing of leaf moisture, as noted by Nelson et al. (2015). However, quailbush in irrigated or subirrigated areas in the LCR ecosystem may not experience seasonal deficits in quailbush leaf moisture. The effects of larval growth on larval survival are thus complex and affected by other factors that determine whether the larvae in a cohort aestivate. The hypothesized link is proposed to be unidirectional and is proposed to have high intensity and spatial and temporal scales: The relationship is biologically highly plausible. However, the literature provides no information on how precisely MNSW egg growth may affect survival. Link predictability is unknown and link understanding low. *Applies to Larvae.*

## SUMMARY OF STANDARDIZATION OF TERMS

(Items highlighted in blue were added or revised for 2018; items highlighted in orange indicate replaced items).

Table 5.—(New table for this update): Updated MNSW conceptual ecological model component names

MNSW conceptual ecological model updated terms, 2018	MNSW conceptual ecological model original terms, 2015
<b>Life stages</b>	
Eggs	Egg
Larvae	Larval
Pupae	Pupal
Adults	Adult
<b>Life-stage outcomes</b>	
Egg Survival	Egg Survivorship
Egg Growth	(New)
Larval Survival	Larval Survivorship
Larval Growth	(New)
Pupal Survival	Pupal Survivorship
Adult Survival	Adult Survivorship
Adult Fertility	Reproductive Output Rate
Adult Dispersal	Adult Dispersal Rate
<b>Critical biological activities and processes</b>	
Chemical Stress	(Formerly under Contamination and Infection)
Competition	(New)
(eliminated; see Chemical Stress, Disease)	Contamination and Infection
Disease	(formerly under Contamination and Infection)
Foraging	Feeding/Watering
Mating	Mating
Mechanical Stress	(Formerly under Physiological Stress)
Ovipositing	Ovipositing
(eliminated; see Mechanical, Thermal Stress)	Physiological Stress
Predation	Predation
Resting/Hiding	Hiding/Resting
Thermal Stress	(Formerly under Physiological Stress)
<b>Habitat elements</b>	
Arthropod Assemblage	(Formerly under both Competitors and Predators)
Chemical Contaminants	Chemical Contaminants
(eliminated; see Arthropods, Vertebrates)	Competitors
Fire Regime	Fire Regime
Herbaceous Vegetation Assemblage	(New)
Infectious Agents	Infectious Agents
Inundation Regime	Inundation Regime
(eliminated; see Woody, Herbaceous vegetation)	Nectar Sources
Monitoring, Capture, Handling	Scientific Study
(eliminated; see Arthropods, Vertebrates)	Predators
Quailbush Litter Condition	Quailbush Litter Condition
Quailbush Patch Distribution	Quailbush Patch Distribution
Quailbush Patch Size and Structure	Quailbush Patch Size and Structure
Quailbush Shrub Condition	Quailbush Shrub Condition
Soil Moisture	Soil Moisture
Soil Nitrogen	Soil Nitrogen
Soil Salinity	Soil Salinity
Vertebrate Assemblage	(Formerly under both Competitors and Predators)
Woody Vegetation Assemblage	(New)
<b>Controlling factors</b>	
Offsite Land Management and Use	Offsite Land Management and Use
Onsite Fire Management	Onsite Fire Management
Onsite Vegetation Management	Onsite Vegetation Management
Onsite Visitation and Study	Onsite Visitation and Study
Onsite Water Management	Onsite Water Management
Water Storage-Delivery System Design and Operations	Reach-Scale Water Management



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