Conservation and Management of Western Monarchs on DoD Lands: Implications of Breeding Phenology

Final report for the Department of Defense Legacy Natural Resources Program

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DoD Legacy Natural Resources Program: NR 17-836

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Photo: Stephanie McKnight/Xerces Society.

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Cover photograph

Monarchs mating. (Photograph: Stephanie McKnight/Xerces Society.)

CONTENTS

Acronyms and Abbreviations

AFB = Air Force Base

BMP = Best Management Practice

DoD = Department of Defense

ESA = Endangered Species Act

GAMs = Generalized Additive Models

INRMPs = Integrated Natural Resources Management Plans

JBLM = Joint Base Lewis McChord

MAFWA = Midwest Association of Fish and Wildlife Agencies

MLMP = Monarch Larva Monitoring Project

NAS = Naval Air Station

NRCS = National Resources Conservation Service

NWR = National Wildlife Refuge

NWSTF = Naval Weapons Systems Training Facility

USFWS = US Fish and Wildlife Service

WAFWA = Western Association of Fish and Wildlife Agencies

WSU = Washington State University

EXECUTIVE SUMMARY

Monarch butterflies have declined dramatically across North America and are under review for Endangered Species Act protection. Monarchs which breed west of the Rockies occur broadly and are distinct from the larger eastern population. Monarchs in the West have declined by over 99 percent since the 1980s, with a sharp population crash observed in 2018. They overwinter in California and Mexico, and breed and migrate across the West, including a considerable portion of Department of Defense (DoD) land. Breeding phenology differs between eastern and western populations. Eastern monarchs breed in successively northbound generations. Western monarchs do not follow this pattern, and we lack basic information to construct management strategies that reduce conflict with active military training.

The primary purpose of this work is to determine seasonal timing of monarch butterflies in locations across the West, and to use this information to increase the efficiency and effectiveness of managing habitat for monarchs on DoD lands. This will help DoD land managers maximize the use of these lands for training while considering the needs of a widespread at-risk species.

We used systematic surveys across the breeding range in 2017 and 2018 to gain understanding of seasonal timing of monarch breeding across the West. We conducted monthly surveys—about the time it takes for monarchs to complete one generation—throughout the expected breeding season at five installations in the West and documented abundance of monarch life stages (eggs, larvae, pupae and newly emerged adults)

A monarch larva eating the buds of *Asclepia speciosa* (showy milkweed). Photo: Stephanie McKnight/Xerces Society.

as evidence of site-based breeding phenology. The five installations include Vandenberg Air Force Base (AFB) in California, Naval Weapons Systems Training Facility (NWSTF) Boardman in Oregon, Joint Base Lewis McChord (JBLM) Yakima Training Center in Washington, Naval Air Station (NAS) Fallon in Nevada, and Mountain Home AFB in Idaho. In addition, we surveyed near US Army Corps of Engineers sites in northern California. We used Generalized Additive Models (GAMs) to understand monarch breeding phenology. Because our work spans a broad geographic area, our approach allows us to make inference about the western monarch population from relatively sparse data and acts as a building block for constructing a demographic model of western monarchs in future work.

We learned the following from our surveys and associated analyses

- Western monarchs breed throughout the season consistent with a population which expands in distribution throughout the breeding season rather than one that shifts throughout the breeding season
- Milkweed diversity within a region is a key component of western monarch habitat
- Monarchs are selective in their use of milkweeds. When multiple milkweed species were available, monarchs selected *A. cordifolia, A. incarnata* and *A. speciosa* more often than other available milkweed species in some years and other years were not selective.
- At the rangewide scale, milkweed does not appear limiting nor was it likely to be a primary factor responsible for the 2018 crash. However, at local scales and at critical times of year (spring), milkweed may be limiting
- We see evidence of a marked decline in abundance before the beginning of the 2018 breeding season, indicating that factors responsible for the 2018 crash occurred before the beginning of the breeding season.

These findings have direct application to DoD natural resource management including

- Installation management of monarch breeding habitat is not linked to the 2018 population crash because the causal drivers of the crash likely occurred before the beginning of the 2018 summer breeding season
- Across the West, broad landscape-scale milkweed limitation in the breeding range is not a dominant driver of the recent population crash in 2018
- Enhancement of breeding habitats at key times of year (spring) and/or in key regions (California's Central Valley) might contribute to population recovery
- We developed regional windows for seasonal timing of habitat management to balance training needs with use of breeding habitat by monarchs
- We developed installation-specific guidance for Integrated Natural Resources Management Plans (INRMPs) within our Best Management Practices document
- Continued sparse but systematic monitoring across the western landscape provides an important window into monarch population dynamics and can provide broad guidance for installations if the monarch is protected under the Endangered Species Act.

Understanding monarch habitat use on DoD installations is crucial to maximizing proactive management for monarchs while minimizing interruption of operations. Continued and future programs such as this one provide a basis for tailoring management to ecosystem and species needs in balance with mission of installations for DoD use of the lands.

INTRODUCTION

The monarch butterfly (*Danaus plexippus plexippus*) has experienced dramatic declines across North America. Western monarchs, which overwinter in coastal California, declined by 97% between the 1980s and the mid-2010s; and in 2018, the population dropped even further for a total estimated decline of >99%. Current trends indicate a quasi-extinction risk of 72% in 20 years and 86% in 50 years (Schultz et al. 2017; Pelton et al. 2019). This is far greater than the decline observed in the eastern monarch population, which overwinters in central Mexico and has declined by an estimated 80% since the mid-1990s; the eastern population has a quasi-extinction risk of 11-57% in 20 years (Semmens et al. 2016). Declines in western monarchs have been documented in both declines in the overwintering sites and in spring and summer monitoring over the past 40 years along a latitudinal transect that spans Northern California (Espeset et al. 2016).

As monarch populations have rapidly declined in a single human generation, many are wondering what they can do to save the monarch and its milkweed host plant. While guidance to answer this question for monarchs is in development for the eastern and central areas of the U.S. (see *Monarch Joint Venture's Mowing for Monarchs*, the Natural Resources Conservation Service (NRCS) and US Fish and Wildlife Service's (USFWS) *Monarch Butterfly Conference Report*, and Midwest Association of Fish and Wildlife Agencies' (MAFWA) *Mid-America Monarch Conservation Strategy 2018-2038)* guidance for how land managers can conserve and revive monarch populations in the western U.S. has only recently been developed (see Xerces' *Managing for Monarchs in the West* and Western Association of Fish and Wildlife Agencies' (WAFWA) *Western Monarch Butterfly Conservation Plan 2019-2069)*. This lack of guidance has been due in part to lack of knowledge about when and where monarchs occur in the landscape across the West.

This project addresses a key part of this gap by investigating the seasonal timing of monarchs across the West. We conducted field surveys 2017 and 2018 across five military installations in the West (Vandenberg AFB in California, NWSTF Boardman in Oregon, JBLM Yakima Training Center in Washington, NAS Fallon in Nevada, and Mountain Home AFB in Idaho). Based on our analyses, we developed broad management recommendations and windows for managing existing monarch habitat and, where appropriate, restoring habitat on military installations in the West.

Monarchs mating. Photo: Stephanie McKnight/Xerces Society.

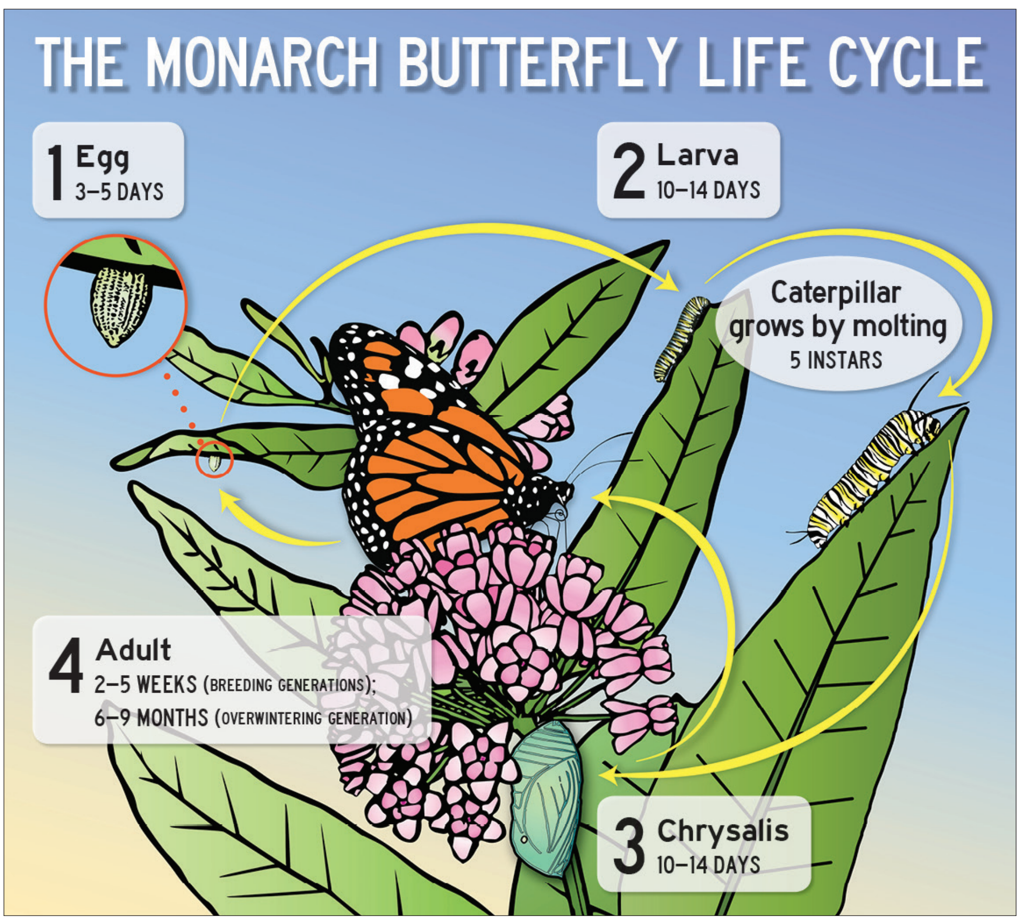
MONARCH BIOLOGY

Life Cycle

Like all butterflies, the monarch's life cycle includes eggs, caterpillars, pupae and adults (Figure 1). Within an annual cycle, monarch butterflies complete multiple generations, with breeding several times throughout each season. Focal resources for butterflies include hostplants for growing caterpillars and nectar flowers which provide nutrition for adults.

Female monarchs lay eggs on milkweed (*Asclepias* spp.) and related plant genera. Caterpillars (larvae) rely on milkweeds as their sole source of food as they develop through five instars. Milkweed also provides the caterpillars with cardenolides—toxic compounds that make them unpalatable to many vertebrate predators. Their bright, aposematic coloration warns predators of their toxicity. However, parasitism and predation of caterpillars by invertebrates can be high—with less than 10% of eggs typically surviving to adulthood (Nail et al. 2015). Fifth instar caterpillars form a cryptic green chrysalis (pupa) with gold trim and attach to milkweed, surrounding vegetation, or other structures. A few days later, the adult butterfly emerges and quickly becomes mobile to find a mate and nectar on flowers, with females searching for milkweed upon which to lay their eggs. Multiple generations are produced over the spring and summer, with the fall generations migrating to overwintering sites. Spring and summer generations typically live 2-5 weeks as adults while overwintering butterflies may live 6-9 months.

Figure 1: Monarch butterfly life cycle. Diagram: Sara Morris/Xerces Society.



Migration and Distribution

Monarchs are found throughout North America, as well as Hawaii, other Pacific Islands, Australia, New Zealand, Spain, and Portugal. In North America, where monarchs are most numerous, they migrate traveling hundreds or thousands of miles from their breeding grounds found across the U.S. and into southern Canada (about 50° North) to overwintering grounds in both Mexico and California. The eastern monarch population—defined as monarchs that breed east of the Rocky Mountains—migrate to and overwinter in high-elevation oyamel fir forests in the states of Michoacán and Mexico, both in central Mexico. The western monarch population, which breeds west of the Rocky Mountains, migrates to and overwinters in forested groves along the Pacific coast stretching from Mendocino, California, south into western Baja, Mexico as well as central Mexico. Considerable debate exists around the degree of genetic relatedness between eastern and western monarch (Lyons et al. 2012). However, there is considerable evidence that eastern and western monarchs are ecologically and phenotypically distinct (e.g., Altizer and Davis 2010, Freedman et al. 2018). In addition to these major overwintering sites, small numbers (under 100 butterflies at any one site) of butterflies overwinter in the Saline Valley of California (Xerces Society Western Monarch Thanksgiving Count 2018), Sonoran desert near Phoenix, Arizona (Morris et al. 2015), and the Mojave desert near Lake Mead, Nevada (Gail Morris, personal communication, January 2018). There are also smaller, non-migratory populations in Florida and other parts of the extreme southern United States.

Each spring, monarchs leave their overwintering grounds to seek out milkweed in their spring and summer breeding range—which is broadly distributed across the United States as far north as Southern Canada. In the West, monarchs are thought to breed continuously from spring through fall in California, Nevada, and Arizona and subsequent generations continue to travel north and east into the interior of the continent throughout the summer (James 2016).

As fall approaches, native milkweeds senesce and monarchs start to migrate to the overwintering grounds rather than reproduce. The migratory generation(s) use the earth's magnetic fields, a time-compensated sun compass, and likely other cues to start flying south (Heinze and Reppert 2011). In the West, monarchs generally migrate in a dispersed manner, but sometimes large aggregations are spotted— especially in nectar- and water-rich areas in the arid West. Dingle et al. (2005) found a strong association of monarch collection record location and close proximity to rivers, and proposed that western monarchs use rivers as major migratory corridors since they provide more reliable sources of water, nectar, and overnight roosting trees. Anecdotes of monarchs forming temporary aggregations in trees along rivers and in suburbia to spend the night or take shelter from storms have been reported from Arizona in the fall (Gail Morris, personal communication, January 2018). Once the butterflies reach their overwintering grounds—typically in September or October in California; October or November in central Mexico—they form clusters with other butterflies to conserve warmth and settle in for the months ahead. An isotopic study demonstrates that monarchs at California overwintering sites arrive from all regions of the West—including a large portion coming from interior western states (Yang et al. 2016, James et al. 2018). Overwintering monarchs in California are typically in reproductive diapause—conserving their fat for survival and spring dispersal—until February or March. One exception is the coastal area of southern California (in Santa Barbara and southward) where the widespread planting of non-native, tropical milkweed (*A. curassavica*) and a mild winter climate has led to year-round breeding and possibly the modification of overwintering behavior (Satterfield et al. 2018). Monarchs are also known to breed year-round on native, evergreen milkweeds in parts of Arizona (Gail Morris, personal communication, January 2018).

Breeding Habitat

Breeding monarchs require larval and adult resources as well as habitat structures to promote their growth and development.

Potential breeding habitat for monarchs is defined by presence of milkweed. Milkweed grows in a variety of habitat types from barren desert slopes to wet meadows in both disturbed and undisturbed areas. Some milkweed species are adapted to natural disturbances, and are commonly found on roadsides, along irrigation ditches or canals, in or adjacent to irrigated agricultural fields, in burned areas, or along stream or river banks, while others may be more sensitive to disturbance and have more specific habitat associations. Western monarch eggs and caterpillars have been observed in all of these habitat types.

Milkweed in the west includes 23 species in the six states included in this project (see Figure 2). The primary limits to milkweed distribution are elevation and proximity to the Pacific Coast. Milkweeds generally do not occur above 9,000 feet throughout the study region, with one exception, Hall's milkweed (*A. hallii*), in Nevada. At this time, we lack data on the use of high elevation milkweed species by monarchs as larval hosts. Six milkweed species were encountered in our study areas (see Box 1). Information on additional milkweed species in the West can be found in an appendix of our companion document, *Monarch Conservation on Department of Defense Lands in the West: Best Management Practices*.

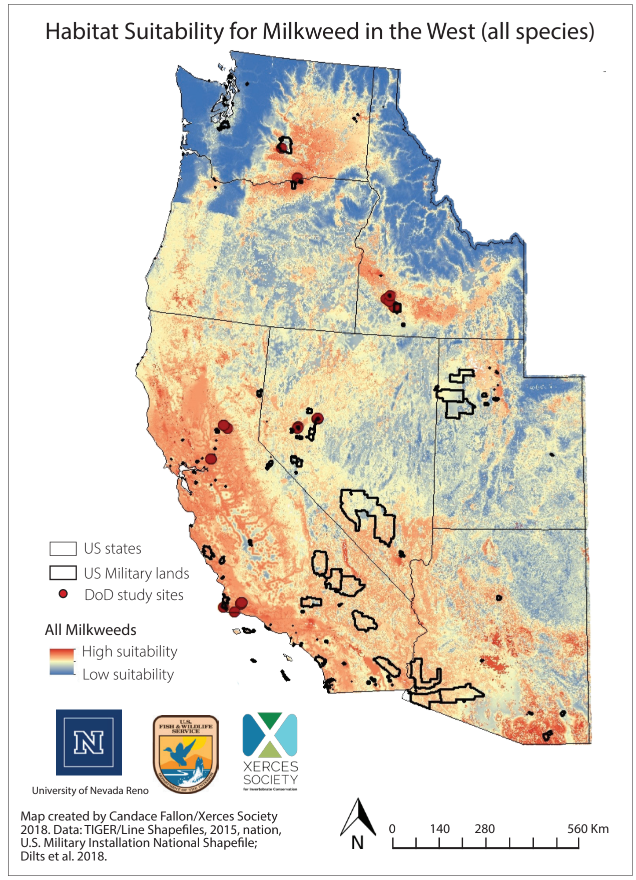


Figure 2: Habitat suitability for milkweed in the West with US military lands and study sites outlined.

Asclepias fascicularis (narrowleaf milkweed) in shaded habitat. Photo: Cameron Thomas/Washington State University.

Box 1: Milkweed species documented on DoD lands.

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Asclepias cordifolia (heartleaf milkweed)

This milkweed grows in dry, rocky areas in woodlands, chaparral, and evergreen forest It is also found on slopes and hillsides in rocky or gravelly soil in chaparral, juniper woodland, shrub steppe, and open pine and fir forests and on lava flows. Typical phenology is April–July. This milkweed was encountered in Northern California study areas.

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Asclepias cryptoceras (pallid milkweed)

This milkweed grows in dry, open, barren places such as washes, slopes, and hillsides, in pinyon-juniper woodland, sagebrush communities, salt desert shrublands, and aspen zones. May grow in clay, sand, gypsum, or serpentine soils. Typical phenology is from April–June. This milkweed was only encountered in Idaho study areas.

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Asclepias eriocarpa (woollypod milkweed)

This milkweed grows in dry, rocky areas in many plant communities, including valley grassland, chaparral, and foothill woodland. It also grows along stream banks and roadsides. Typical phenology is May–October. This milkweed was only encountered in California study areas.

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Asclepias fascicularis (narrowleaf milkweed)

This milkweed is widely distributed across the West. This milkweed grows in grasslands, wetland-riparian areas, woodlands, and chaparral. In the Great Basin it grows in pinyon-juniper, sagebrush, and mountain brush communities, and moist to dry places including stream banks, roadsides, the banks of irrigation ditches, and fallowed fields. Typical phenology is from April–October, depending on region. This milkweed was encountered in study areas in California, Nevada and Oregon.

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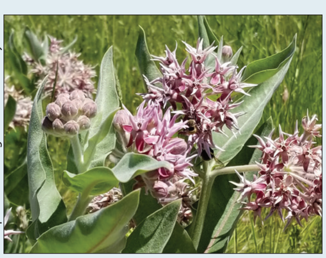
Asclepias incarnata (swamp milkweed)

This milkweed grows in wet, flat, grassy meadows as well as streams and ditchbanks, marshes, and moist or wet ground and is occasionally found growing in water. Typical phenology is from June–August. This milkweed was only encountered in Idaho study areas.



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Asclepias speciosa (showy milkweed)

This milkweed is widely distributed across the West. It grows in dry to moist soil in open, sunny areas and occurs in many plant communities including wetlands, meadows, savannah, and forest clearings, as well as disturbed sites along roadsides, railways, and waterways. It is widely tolerant of alkaline soils and can become weedy in cultivated fields, pastures, and along roadsides, railways, and around habitations. Typical phenology is from May–September, depending on region. This milkweed was encountered in all study regions except Southern California.

In addition to larval resources, monarchs require sufficient nectar resources throughout the breeding season. During peak flowering season, monarchs often nectar on milkweed flowers. However, monarchs, like many butterflies, are nectar generalists and will nectar on a diversity of wildflower species. Over 150 different nectar plant species have been reported as being used by monarchs in the West (Xerces Society, unpublished data). Milkweeds (*Asclepias* spp.) make up about a third of all nectaring observations reported, highlighting their importance not only as caterpillar hosts but also as nectar sources for adults. In butterflies, sufficient nectar enhances both adult survival and female fecundity (O'Brien et al. 2004). Because western monarchs may fly great distances between oviposition events, providing enough fuel to support these dispersal events may be critical to supporting the population. However, detailed understanding on required diversity and abundance of nectar is lacking,

Finally, habitat structure may be critical to successful breeding in many parts of the western monarch range. Western habitats have a great diversity of climates, soil times and ecological environments. Observations suggest that monarchs may prefer areas that are close to riparian areas or wetland seeps, especially in arid parts of the West (Dingle et al. 2005). In addition, monarchs are often attracted to trees and shrubs which may provide shade and roosting structure. Like nectar, greater understanding about relative importance of these factors for western monarchs would substantially help managers and installation biologists in planning efforts to protect and enhance habitat for monarchs.

Monarch nectaring on rabbitbrush. Photo: Stephanie McKnight/Xerces Society.

THREATS TO WESTERN MONARCHS

The western monarch butterfly faces multiple stressors across its range (Crone et al. 2019b). Threats broadly include loss and degradation of breeding habitat, pesticides, climate change, parasites and diseases (for further discussion of threats, see *Monarch Conservation on Department of Defense Lands in the West: Best Management Practices*). Changes in all of these factors have occurred over the same time period as the decline in the western monarch population. Recent analyses to disentangle these factors suggest the overarching importance of changes in land use (including development and pesticides), which has implications for the importance of local action by managers and installation biologists on efforts to recover western monarchs over the long-term (Crone et al. 2019b).

Monarchs mating. Photo: Stephanie McKnight/Xerces Society.

Monarch chrysalis. Photo: Stephanie McKnight/Xerces Society.

PROJECT OBJECTIVE

Our work advances knowledge to meet emerging threats, as highlighted in the 2017 DoD Legacy Areas of Emphasis: Planning to Address and Adapt to New and Emerging Threats. This includes "mitigation of possible future restrictions to training, testing or operations resulting from species declines, habitat and loss and regulatory actions." If monarchs are listed under the Endangered Species Act (ESA), habitat management could impact nearly all DoD installations. Furthermore, if DoD actively engages in monarch conservation on DoD lands, those efforts—in concert with other monarch habitat conservation efforts on public and private land—may lead to monarch recovery and eliminate the need to list the species under the ESA. Efficient and effective species conservation planning require knowledge of essential aspects of a species' biology.

Recovering at-risk species requires managing habitat throughout a species' life cycle; central to this goal is an understanding of basic phenology (timing of major life history events). Earlier studies of western monarch posit a range of potential population structures and migration strategies. Wenner and Harris (1993) suggest that monarchs overwintering in coastal California primarily expand their range during warmer times of year and contract during cooler times, a hypothesis termed the *local recruitment* hypothesis (Wenner and Harris 1993, Stevens and Frey 2010). Alternatively, long-distance migration has been hypothesized in prior decades, including classic tagging studies by the Urquharts and colleagues in which tagged butterflies from inland locations were observed wintering in coastal California (Urquhart and Urquhart 1977), the *long distance migration* hypothesis. Moreover, within the global distribution of monarchs, populations are known to exhibit *complete migration*, in which breeding and non-breeding generations do not overlap, *non-migratory* or *resident populations*, in which the population is resident year-round, and *partial migration*, in which some individuals migrate away from the wintering grounds and others are resident year-round (James 1993, Dingle et al. 2005, Malcolm 2018, Satterfield et al. 2018). Recent studies reinforce the importance of long-distance migrants to the coastal overwintering populations. James et al. (2018) recovered tagged individuals from distant locations in Oregon, Washington and Idaho in coastal California. In addition, isotopic studies by Yang and colleagues indicate as much as ⅓ of the overwintering population may originate in these distant sites (Yang et al. 2016).

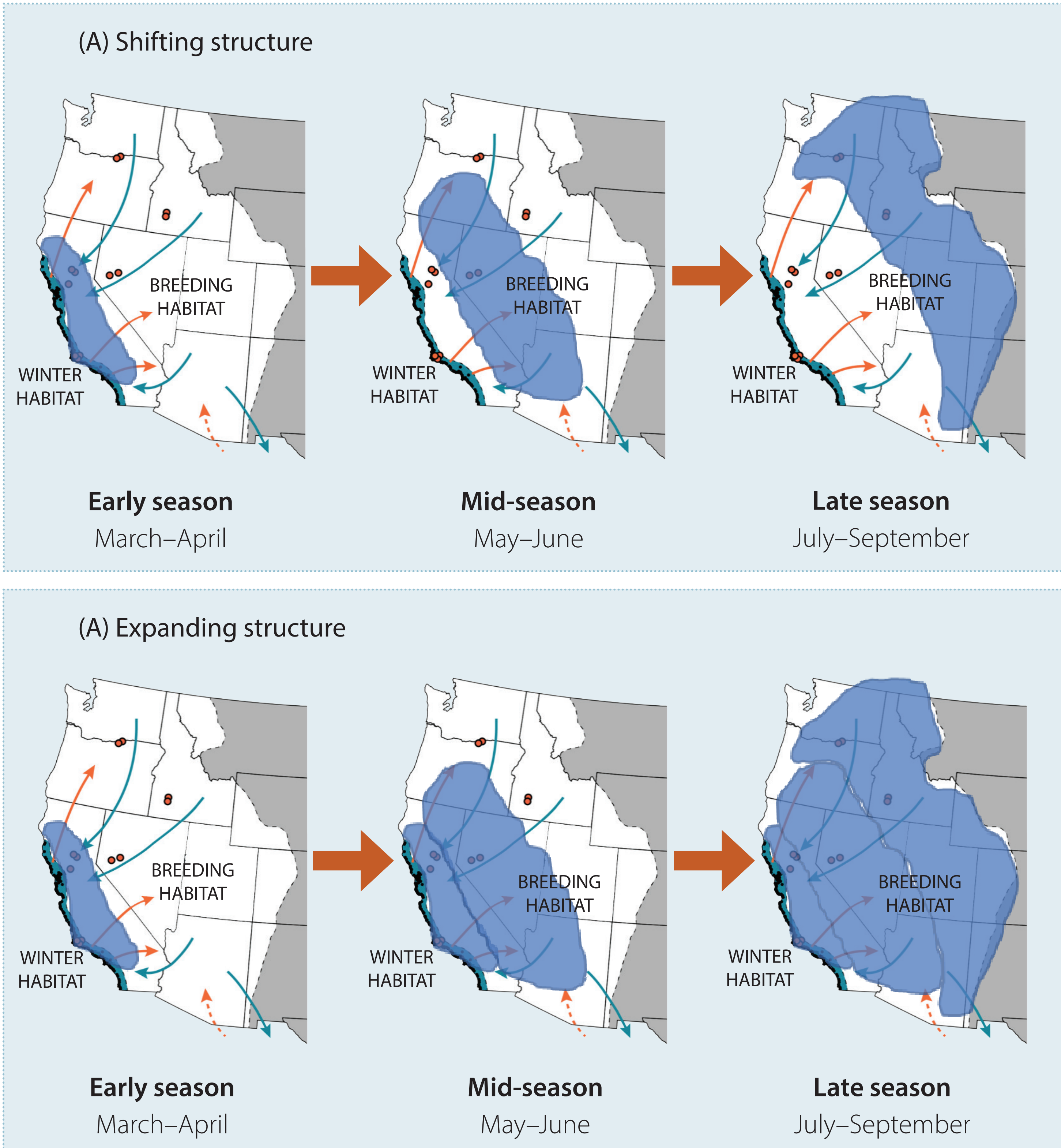
Thus, the preponderance of studies consistently support long-distance migration as an important component of the western migratory population (Nagano et al. 1993, Dingle et al. 2005, Yang et al. 2016, James et al. 2018). However, these studies do not discriminate between a shifting population structure during the breeding season and an expanding population structure. Monarchs have multiple overlapping breeding generations throughout the year and key resources can limit how large local populations can grow over the course of a single breeding season. Eastern US monarchs largely avoid this challenge by spatially separating discrete generations. In short, eastern monarchs that overwinter in Mexico breed in successive north-moving waves, with a first generation in the southern US in spring, second and third generations in the central US in early summer, a fourth and possibly fifth generation in the central US, New England, and southern Canada in late summer and early fall (Flockhart et al. 2013). For eastern monarchs, a detailed "compartment" model of larval and adult demography across breeding locations provides land managers with guidance for when and where to prioritize habitat management for breeding monarchs. This model is the backbone of a population model from which biologists can predict population decline and extinction risk, and evaluate the effect of alternative conservation plans on population dynamics. In contrast, for western monarch we lack information on the seasonal structure of the breeding population to discriminate between a *shifting* population structure and an *expanding* population structure (Figure 3), which is critically important to managers in implementing on-the-ground efforts timed to minimize impacts on at-risk populations. Understanding the breeding phenology is vital to guiding efficient management actions, especially to directing timing to reduce conflict with military training and operational use of DoD lands.

The objective of our work is to fill major gaps about western monarch breeding biology and phenology to facilitate management of western monarch populations by DoD Natural Resource managers. To do so, we monitored monarch habitat (e.g., known host plant populations) at selected DoD sites that span the region known to make significant contributions to the overwintering population in coastal California. Our region of interest is based on work indicating that one third to one half of overwintering monarchs in California breed in Oregon, Washington and/or Idaho, and likely have spring migration and breeding populations that move through California and Nevada (Yang et al. 2016).

Monarch caterpillar on *Asclepias cordifolia* (heartleaf milkweed). Photo: Stephanie McKnight/Xerces Society.

Figure 3: Cartoon of breeding season population structure.

(A) Shifting structure, (B) Expanding structure.



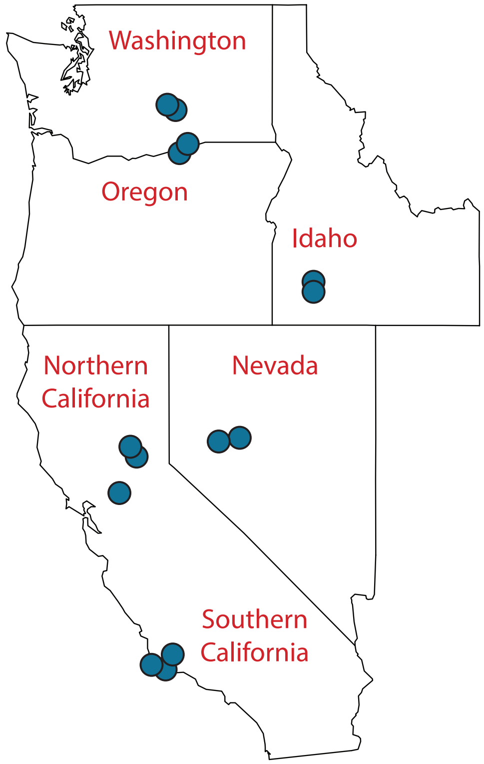


Figure 4: Survey sites within 6 regions: Southern California, Northern California, Nevada, Idaho, Oregon and Washington.

PROJECT METHODS

We conducted monthly surveys (about the time it takes for monarchs to complete 1 generation from egg to adult) throughout the expected breeding season in 6 regions at DoD installations and nearby areas (Southern California, Northern California, Nevada, Idaho, Oregon and Washington Figure 4). In each region, we selected a study area at the focal DoD installation as well as nearby natural areas to capture the range of potential high quality monarch breeding habitat in the region. Study areas were initially identified based on presence of milkweed in historic and current records, as collated in the Xerces Society Western Milkweed and Monarch Mapper (www.monarchmilkweedmapper.org) and groundtruthed with visits in early 2017. We documented abundance of all monarch life stages (eggs, larvae, pupae and newly emerged adults) as evidence of site-based breeding phenology.

Project Installations and Nearby Sites

Southern California - *Vandenberg AFB, Gaviota State Park, and Sedgwick Reserve*

Vandenberg Air Force Base (34.61 N, 120.59 W) and Gaviota State Park (34.47 N, 120.23 W) are west of Lompoc and north of Goleta in southern California along the coast of the Pacific Ocean. Sedgwick Reserve (34.69 N, 120.04 W) is 60 km east of Vandenberg AFB just outside of Los Padres National Forest. Vandenberg AFB and Gaviota State Park are coastal scrub habitats along the Pacific Coast containing plants such as coyote bush and California buckwheat. Sedgwick occurs in Valley oak savannah and grey pine forests of the Coastal Mountain range. *Asclepias fascicularis* occurs in small single patches on Vandenberg AFB and Gaviota State Park, and *A. fascicularis* and *A. eriocarpa* occur in small scattered patches at Sedgwick Reserve. All Southern California sites were surveyed once per month. In 2017 we conducted 6 surveys, from late April to early October and in 2018 we conducted 8 monthly surveys from late March to early October.

A. eriocarpa. Photos: Stepahnie McKnight/Xerces Society.

Northern California – *South Yuba State Park, Grass Valley, and Stone Lakes NWR*

South Yuba River State Park (39.29 N, 121.19 W) is approximately 50 km east of Yuba City in Northern California and follows the South Yuba River; Grass Valley, CA (39.21 N, 121.04 W) is 15 km southeast of South Yuba River State Park; and Stone Lakes National Wildlife Refuge (38.36 N, 121.49 W) is approximately 25 km south of Sacramento, CA. South Yuba State Park and Grass Valley occur in the Central California Foothills with mixed forests of Ponderosa pine, gray pine, and deciduous oak trees. *Asclepias cordifolia* and *A. fascicularis* both occur at South Yuba in small isolated patches along moderate to steep slopes and roadsides above the South Yuba River. *Asclepias speciosa* and *A. eriocarpa* occur in small patches in an open meadow. Stone Lakes NWR is in the Central Valley, and *A. fascicularis* occurs in small to large patches in seasonal wetlands and on the margins of perennial wetlands. All Northern California sites were surveyed once per month. In 2017 we conducted 6 monthly surveys, from late April to early October and in 2018 we conducted 8 monthly surveys from late March to late October. The project has been funded for a third year. In 2019, Beale AFB was included in the surveys.

A. fascicularis. Photos: Stepahnie McKnight/Xerces Society.

Nevada – *NAS Fallon, Stillwater NWR, and Dixie Valley*

Naval Air Station Fallon (39.42 N, 118.70 W) is in western Nevada approximately 110 km east of Reno and just north of Carson Lake. Stillwater National Wildlife Refuge (39.51 N, 118.51 W) is 15 km northeast of NAS Fallon along the Stillwater Point Reservoir. Dixie Valley (39.67 N, 118.08 W) is located 60 km northeast of NAS Fallon just west of the Central Nevada Bald Mountains. All sites occur in Great Basin intermountain cold desert shrub with small spring fed wetlands, and extensive systems of irrigation ditches and canals. *Asclepias speciosa* and *A. fascicularis* occur in small patches along irrigation ditches, canals, springs, and wetlands at both NAS Fallon and Stillwater NWR. Nevada surveys occurred once per month. In 2017 we conducted 5 monthly surveys, from May to September and in 2018 we conducted 7 monthly surveys from late April to October.

A. speciosa. Photos: Stepahnie McKnight/Xerces Society.

Idaho *– Mountain Home AFB and CJ Strike Reservoir*

Mountain Home Air Force Base (43.05 N, 115.86 W) is in southwestern Idaho just north of the Snake River. Mountain Home AFB occurs in the Mountain Home Uplands of the western Snake River Plain. This region is comprised of arid sagebrush steppe and grasslands with mesic soils, flanking the lower riparian areas and wetlands along the Snake River. Mountain Home AFB has small scattered patches of *Asclepias speciosa* in open disturbed areas and along roadsides in arid sagebrush steppe and grassland, and one small isolated patch of *A. cryptoceras* var. *davisii* on steep rocky slopes in sagebrush steppe. *A. incarnata* occurs in large patches adjacent to *A. speciosa* in emergent wetlands dominated by bulrush, cattail, and large stands of Russian olive trees adjacent to the CJ Strike Reservoir of the Snake River. Mountain Home was surveyed once per month. In 2017 we conducted 4 monthly surveys, from July to September and in 2018 we conducted 5 monthly surveys from May to September.

A. speciosa and *A. incarnata*. Photos: Stepahnie McKnight/ Xerces Society.

Oregon *– NWSTF Boardman and Umatilla NWR*

Naval Weapons Systems Training Facility Boardman (45.75 N, 119.68 W) and Umatilla National Wildlife Refuge (45.89 N, 119.57 W) are in eastern Oregon near and along the Columbia River, respectively. Like the Washington sites, both NWSTF Boardman and Umatilla NWR are on the Columbia Plateau and are characterized by the same floral and faunal communities. NWSTF Boardman is approximately 5 km south of the Columbia River, and *A. speciosa* is the only milkweed species that occurs at the facility. Umatilla NWR spans several kilometers on both sides of the Columbia River, and two species of milkweed, *A. speciosa* and *A. fascicularis* occur in large patches along sloughs that flow into the refuge and in tree stands along the river. Umatilla NWR was surveyed twice per month, and NWSTF Boardman was surveyed once per month. Oregon sites were surveyed from early June to early October in 2017 and from late May to early October in 2018.

A. speciosa on the left, *A. fascicularis* on the right. Photos: Cameron C. Thomas/Washington State University.

Washington – *JBLM Yakima Training Center and Lower Crab Creek*

Yakima Training Center (YTC) (46.67 N, 120.37 W) is located northeast of Yakima, WA and spans between the Yakima and Columbia Rivers. Lower Crab Creek (46.83 N, 119.87 W) is east of the Columbia River adjacent to YTC. Both sites are on the Columbia Plateau, part of the larger Columbia Basin. The Columbia Plateau is characterized by deep loess soils and sagebrush steppe flora common in the arid Intermountain West in the United States. *Asclepias speciosa* is the only milkweed species found at these sites and often occurs near water and near Russian olive or other canopy cover. Yakima Training Center and Lower Crab Creek were surveyed from mid-June to August in 2017 and from mid-June to early October in 2018.

A. speciosa. Photos: Cameron C. Thomas/Washington State University.

Survey Methods

Each selected site was surveyed about once per month throughout the likely breeding season in 2017 and 2018. At sites with limited milkweed (less than 500 stems), surveys included all available milkweed in each survey. At sites with moderate to abundant milkweed, transects were selected in optimal breeding locations. In 2017, transects were 50 m long x 30 cm wide and recorded in 5 m intervals to facilitate repeated search of the same milkweed stems in each survey. Sites included at total of 50–2000 milkweed stems per survey, depending on milkweed species and density. In 2018, transects at some sites were replaced with patch counts in which 2 m x 2 m patches were repeatedly surveyed instead of transects to facilitate repeatability in the survey. In addition, due to non-systematic surveys at Washington sites in 2017 and absence of immature monarchs in 2018, Washington sites are excluded from some of the analyses below. At each monitoring location, the following data were collected: location (latitude and longitude), elevation, shade cover and distance to water. In each surveyed unit, we counted milkweed stems and noted milkweed species and phenological stage of each stem (vegetative, flowering and senescing). We inspected each stem for immature monarchs and noted immature stage (egg, instar 1 – 5, pupa). In addition, number of adult monarchs observed, sex and wing wear were noted during the survey.

PROJECT FINDINGS

1 Expanding vs Shifting Populations

Overview and Analysis

Determining if western monarch has an expanding vs shifting population structure is a primary objective of this project (Figure 3). Our surveys were designed to detect these patterns in the population structure. We fit generalized additive models (GAMs) to the number of immatures (summed over all stage classes) per milkweed stem. These analyses used Poisson family, log-link models with the number of immatures as the dependent variable and an offset of natural log-transformed milkweed stems per plot. We included year as a categorical fixed effect, and a smooth function of day of year. Models were restricted to 4 knots (one fewer than the number of observations at each site in each year. Likelihood ratio tests were used to evaluate statistical significance of year, day of year, and their interaction. We analyzed data from each region separately, since we knew *a priori t*hat monarchs arrive at different times in different regions. To evaluate overall trends among years, we also fit an identical model to data from all sites combined across regions. Models were fit using the gam function in the mgcv package (Wood 2011) in R (R_Core_Team 2018), using default settings except as noted above. Statistical comparisons were done with marginal hypothesis tests, calculated using the lrtest function in the lmtest (Zeileis and Hothorn 2002) package in R.

Monarch nectaring on milkweed. Photo: Stephanie McKnight/Xerces Society.

Results and Discussion

As expected, nearly all analyses showed significant seasonality (i.e., significant smooth term of day of year, Table 1 and Figure 5). In 2017, when monarchs were more abundant, our analyses indicate breeding throughout the season in Southern and Northern California from April–October. In Nevada and Idaho, the breeding seasons were shorter (May–September and June–September, respectively). In Oregon in 2017, there was a distinct pulse in June and another in August, suggesting two distinct generations. Together, our monitoring data are consistent with an expanding population that spreads across the range rather than one that shifts throughout the breeding season (Figure 3). That is, if western monarchs were exhibiting a shifting population structure, we would expect that regions with early spring breeding, such as Southern and Northern California, would have an absence of breeding in the summer. Instead we observe continuous breeding in these areas as the population expands into northern and eastern regions on the West throughout the summer.

We also observe a significant year by region interaction. This suggests that there are differences in when breeding peaks in different regions each year. In 2017 we observed breeding throughout the season in all regions. In 2018, we observed summer breeding in Northern California, Nevada and Oregon but not in Southern California or Washington. Overall, monarch numbers were lower compared to 2017—there was a strong effect of year, which will be discussed in Section 3.

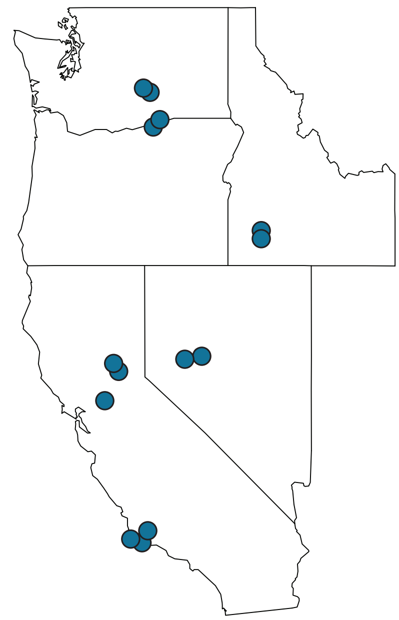
Our efforts were limited to systematic surveys of a few sites per region and therefore limited relative to the vastness of the western landscape. To further resolve these phenological windows within a region would require sampling throughout the breeding season at multiple sites (at least 7-10 sites) within a region rather than 2-4 sites.

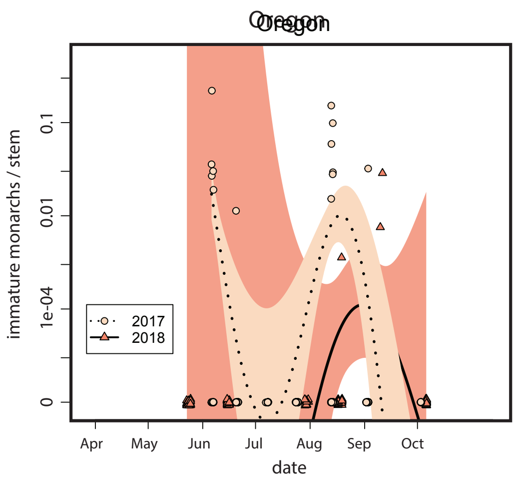
Table 1: Analysis of phenological patterns of monarch butterfly immatures.

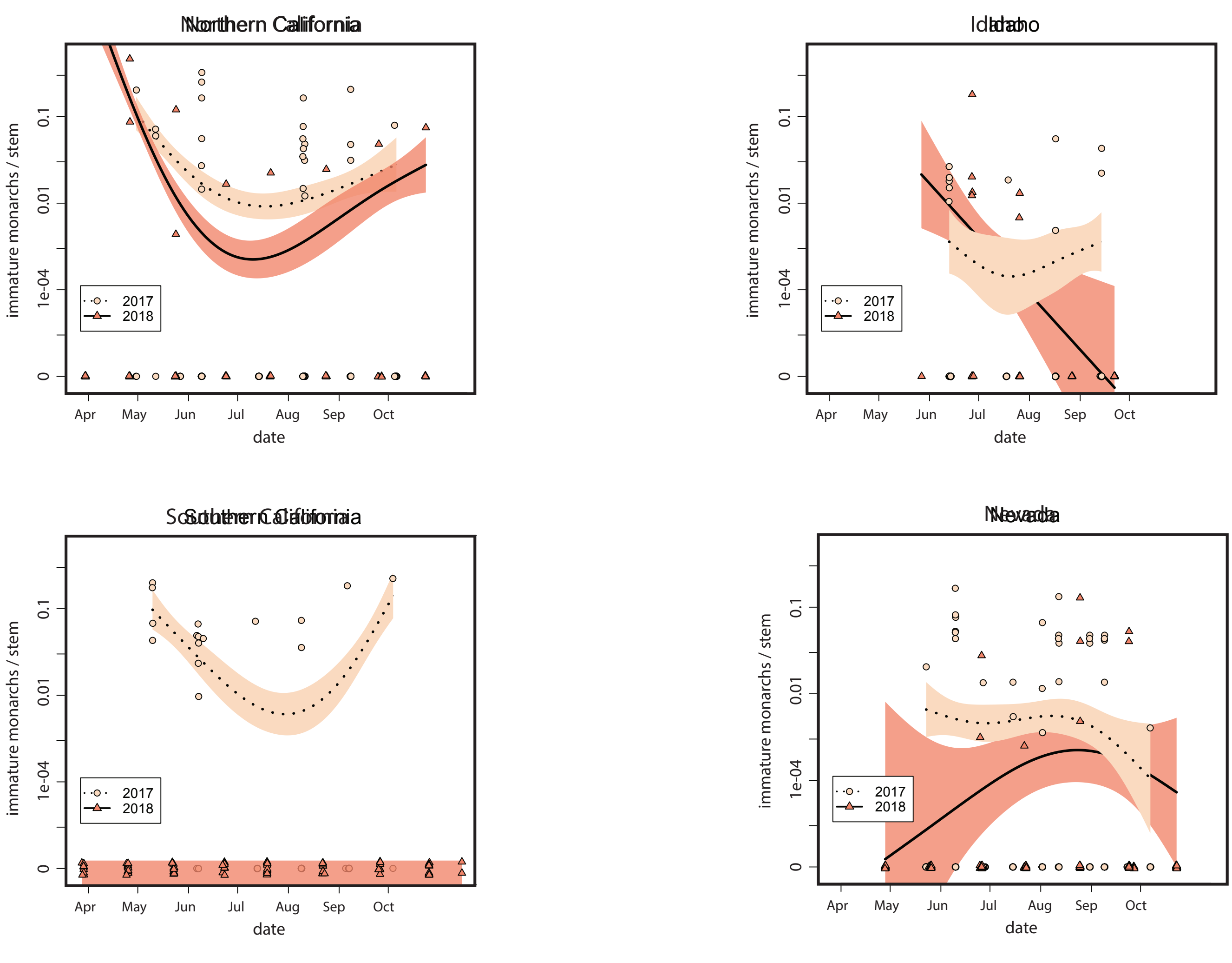
Analysis of Monarch Immatures per Milkweed Stem									
	Year			Day of Year (DOY)			DOY x Year		
Region	$\chi2$	df	P	$\chi2$	df	P	$\chi2$	df	P
Overall	196.9	1.0	<0.001	384.7	2.9	<0.001	2.0	2.8	0.565
Oregon	59.6	1.0	<0.001	22.3	2.9	<0.001	31.4	1.9	<0.001
Idaho	1.0	1.0	0.325	4.0	1.0	0.046	15.1	2.6	0.002
Nevada	14.0	0.8	<0.001	5.2	2.4	0.076	3.0	0.8	0.082
N. California	17.4	1.0	<0.001	212.9	2.9	<0.001	9.3	2.6	0.026
S. California	154.5	1.8	<0.001	59.8	2.7	<0.001	<0.1	1.0	0.990

Figure 5: Immature monarchs/milkweed stem within each region.

Circles = 2017; triangles = 2018, No immature monarchs observed in Washington in 2017 or 2018 so no figure provided.



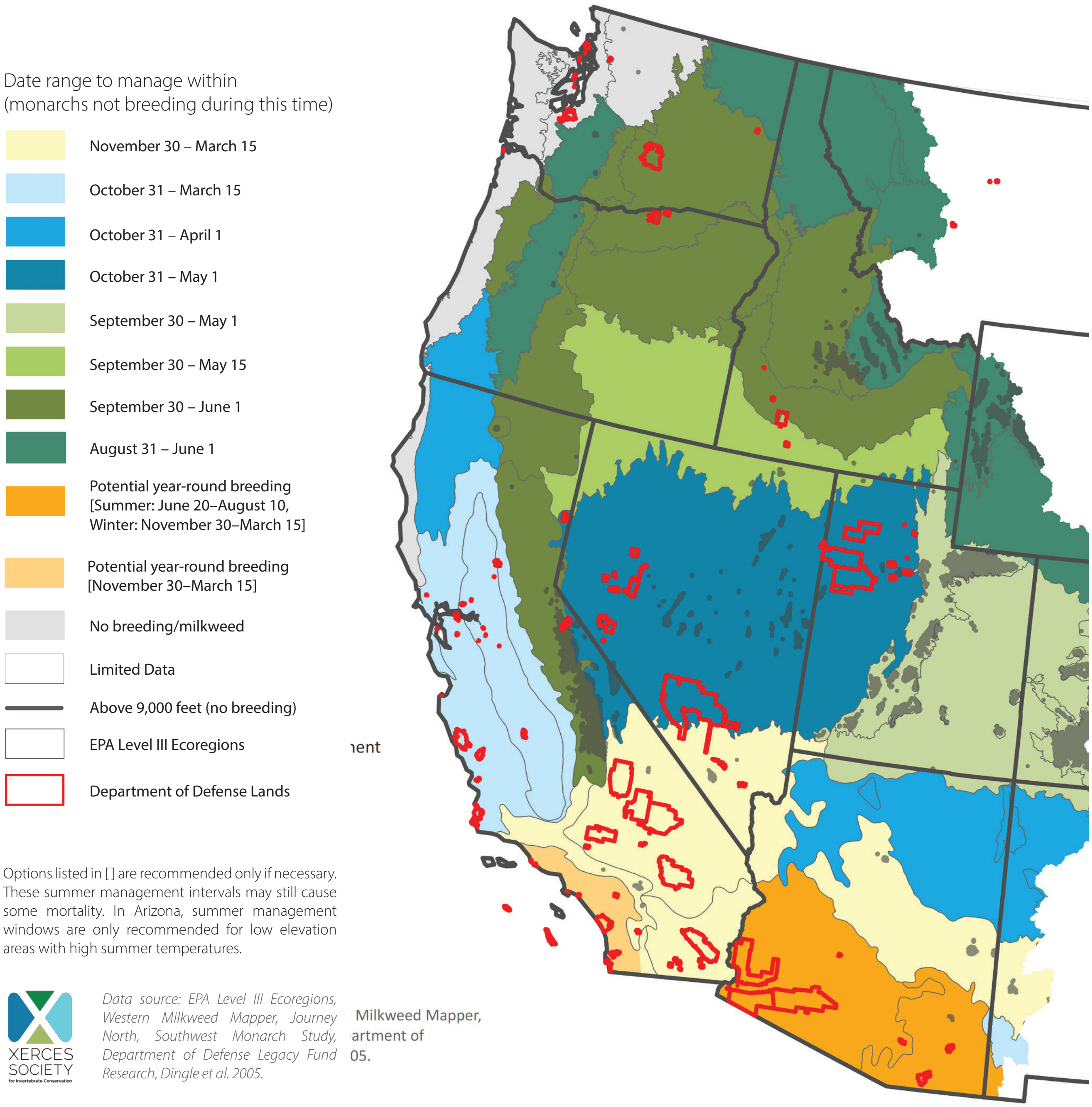




Application

Based on monitoring and analyses to date, we developed a set of management windows (Figure 6) to time management with times when monarchs are not actively breeding in the region. Future monitoring at our focal sites as well as incorporating data from monitoring from other efforts (e.g., Western Monarch and Milkweed Mapper) may help to refine these management windows. We integrated these management windows into broader management strategies in our recent report, *Monarch Conservation on Department of Defense Lands in the West: Best Management Practices*.

FIGURE 6: WESTERN MONARCH MANAGEMENT WINDOWS.



2 Monarch Breeding Habitat Characteristics

Milkweed diversity and its importance for monarchs

Availability of milkweed is a key habitat feature for monarchs to expand their distribution across the West throughout the breeding season. Many herbaceous plant species have a relatively short seasonal phenology and are available as hostplants for butterflies for a few weeks to a few months per year. To support breeding monarchs throughout a several month breeding season, a region may require a diversity of milkweed species with a range of phenologies. Study sites contained one to four milkweed species per region, with the greatest number of milkweed species (Table 2) in Northern California—the region with the longest window of seasonal breeding (Figure 6).

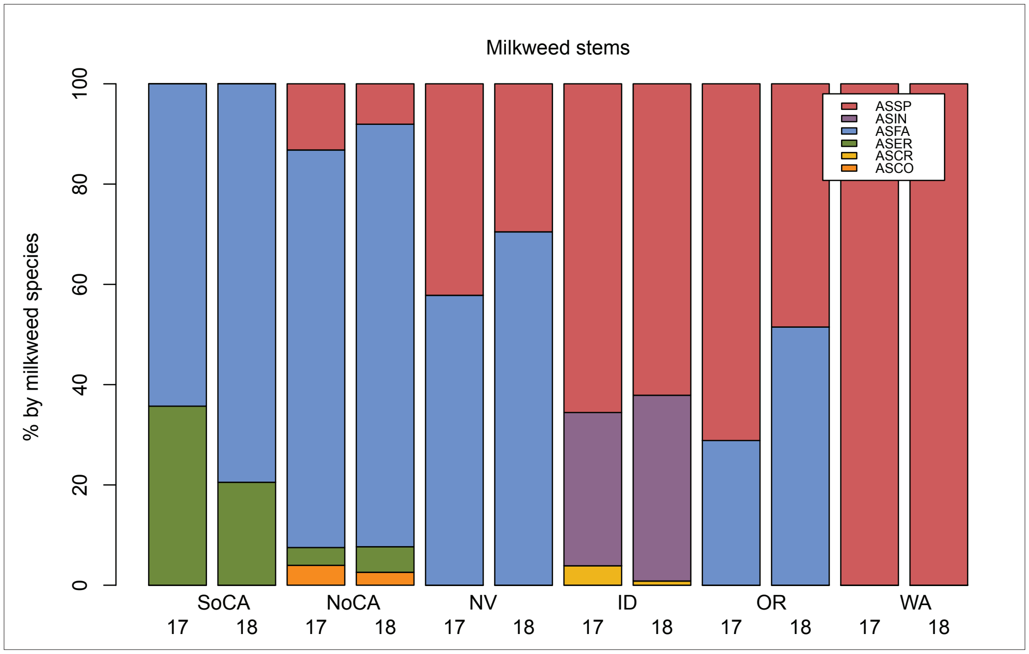
From these surveys, we were interested in understanding the importance of milkweed diversity to monarchs throughout the season. A standard approach in wildlife biology to address questions about the importance of focal resource is an analysis of use vs availability (Manly et al. 2002). In this case, do monarchs use resources in proportion to their availability, or do they use some species more often than expected based on their relative abundance?

Table 2: Milkweed stems counted. ASCO = ***Asclepias cordifolia***, ACSR = ***Asclepias cryptoceras***, ACER = ***Asclepias eriocarpa***, ASFA = ***Asclepias fascicularis***, ASIN = ***Asclepias incarnata***, and ASSP= ***Asclepias speciosa***.

		Species					
State	Year	ASCO	ASCR	ACER	ASFA	ASIN	ASSP
Southern California	2017	0	0	901	1622	0	0
	2018	0	0	803	3108	0	0
Northern California	2017	238	0	213	4761	0	792
	2018	165	0	326	5396	0	516
Nevada	2017	0	0	0	6630	0	4836
	2018	0	0	0	5785	0	2423
Oregon	2017	0	0	0	2062	0	5085
	2018*	0	0	0	13419	0	12641
Idaho	2017	0	288	0	0	2272	4874
	2018	0	59	0	0	2610	4376
Washington	2017	0	0	0	0	0	10430
	2018	0	0	0	0	0	11572

*Surveys in Oregon changed in 2018 to increase the likelihood of encountering immature monarchs (see methods for additional details).

FIGURE 7: MILKWEED STEMS BY GEOGRAPHIC REGION.



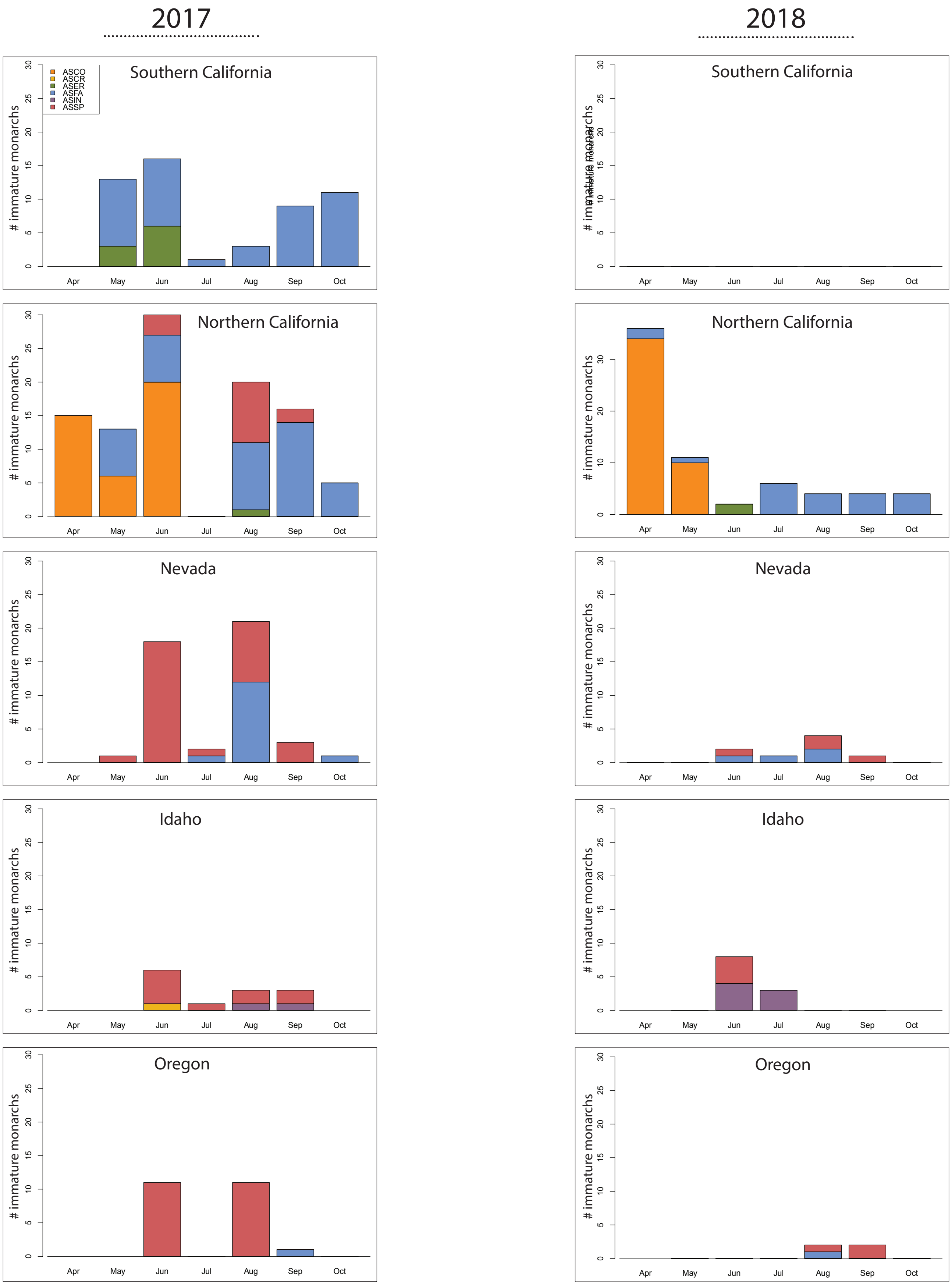
Analytic Methods

For each site-survey, we counted the number of milkweed stems of each milkweed species (Figure 7) as well as the number of immature monarchs on each stem (Figure 8).

We used logistic regression to evaluate use (locations of immature monarchs) vs. availability as follows: First, we calculated the expected proportion of immatures on each species from the proportion of stems of each species in that survey. Then we performed logistic regression with the dependent variable coded as the number of immatures on each species during that survey, relative to the total number of immatures seen in that survey. We converted these numbers into successes (immatures on a target plant), and failures (immatures on all other plant species) notation. We tested whether this proportion differed among milkweed species and whether preferences differed among sites and years by including a fixed effect of milkweed species in binomial family, logit link, GLMs with an offset of the logit-transformed expected proportion. To test whether preferences differed among sites and years, we included site x species, year x species, and site x year x species interactions. (Note that we did not include main effects of site or year because, across species within a survey, the preference by definition sums to one.). For this analysis, we deleted all cases in which availability was 0 (no stems of that species), and all cases in which availability was 1 (only one species seen during a survey). We fit models using the glm() function in R, and tested statistical significance using the Anova() function in the car() package to perform marginal hypothesis tests. This *ad hoc* analysis is more appropriate than standard compositional or ordinal logistic regression models because of the very small numbers of immature larvae observed per survey and the very sparse nature of the milkweed distribution (typically only 1 or 2 species present in a given survey).

From these analyses we calculate selection coefficients for each milkweed species within each region x year combination. To interpret these coefficients, a value of 0.5 indicates no preference for a resource type in given region at the surveyed time. That is, use of a resource is strictly related to its availability. A value greater than 0.5 indicates preference for a resource relative to available resources. For example, if there were 2 stems of each of four milkweed species and monarch immatures were found on 1 stem of each milkweed species, the selection coefficient for all four milkweed species would be 0.5.

FIGURE 8: IMMATURE MONARCHS ENCOUNTERED IN SURVEYS BY MILKWEED SPECIES, REGION, AND YEAR.



Results and Discussion

Our analyses indicate that monarchs select some milkweed species more than others, but that these effects are strongest in some regions (Table 3) and vary by year. Monarchs showed preferential use of *A. fascicularis* in Southern California, *A. cordifolia* in Northern California and *A. speciosa* in Oregon. In addition, in some regions monarchs show preference in one year but no preference in another (e.g., *A. speciosa* in No CA and Nevada and *A. incarnata* in Idaho, Figure 9).

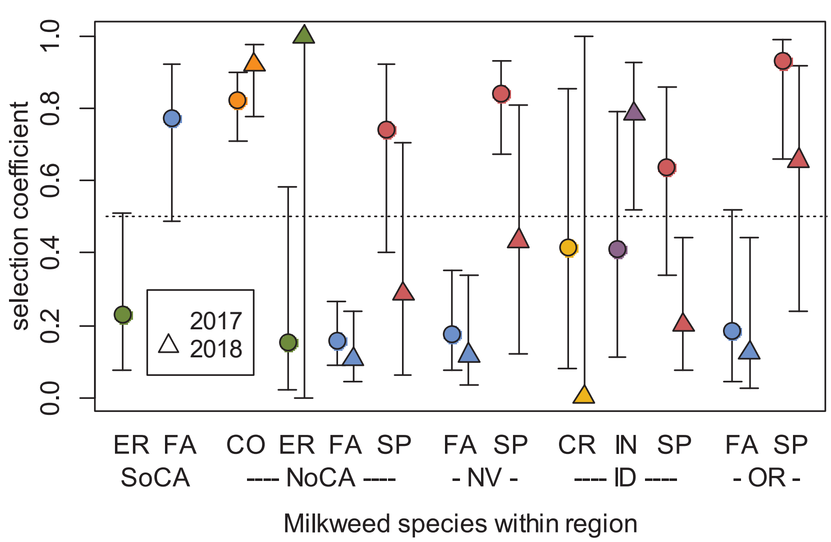
Because the immature monarchs were so scarce in 2018, we have limited ability to detect preference for specific milkweed species in 2018 (i.e., large error bars for selection coefficients in 2018 in OR and NV with less than 5 immatures observed in any survey). This also limits our ability to detect differences between years. It would be valuable to repeat these surveys for multiple seasons to document if monarchs change their use of availability milkweed species in different years, with an understanding that preferences may shift with a changing climate that is predicted to differentially affect the palatability and/or nutrition of available milkweed species (Howard 2018, Svancara et al. 2019).

TABLE 3: ANALYSIS OF USE VS AVAILABILITY OF MILKWEED SPECIES BY IMMATURE MONARCHS.

	χ^2	df	P
Milkweed Species	105.168	5	<0.001 ***
Species x Region	26.672	7	<0.001 ***
Species x Year	20.455	6	0.002 **
Species x Region x Year	5.894	5	0.316

Our results underscore the importance of milkweed diversity in supporting monarchs throughout the breeding season see also (Yang and Cenzer 2019). It also points to the importance of understanding factors (e.g., water, shade) that influence phenological differences in milkweed availability. Moreover, these results point to the importance of availability of monarch habitat at multiple sites and potentially multiple landowners within a region to provide regional habitat heterogeneity for breeding monarchs. Additional fieldwork in 2019 (also supported by the DoD Legacy Program) will contribute to gaining a greater understanding of these factors.

FIGURE 9: SELECTION COEFFICIENT FOR MILKWEED SPECIES WITHIN EACH REGION AND YEAR COMBINATION.



ER = *Asclepias eriocarpa*
FA = *Asclepias fascicularis*
CO = *Asclepias cordifolia*
SP = *Asclepias speciosa*
CR = *Asclepias cryptoceras*
IN = *Asclepias incarnata*

Milkweed abundance and phenology and its importance for monarchs

Resource availability is often a primary focal factor in identifying threats to at-risk species and in developing plans for their recovery. In butterflies, abundance of hostplants is fundamental to maintaining butterfly populations (Dennis 2010). For the eastern monarch, the predominant factor underlying many large conservation efforts is restoring milkweed across the breeding range (Pleasants 2017, Thogmartin et al. 2017). In contrast, a common observation in some parts of the West is that milkweed is abundant and it does not seem to be limiting. Our efforts were not designed to estimate availability of milkweed across the West, rather, we designed these to understand changes in monarch use of available habitat throughout the breeding season. However, We can use our approach to gain a greater understanding of the assumption that abundance and phenology of milkweed limits successful monarch breeding.

In addition, because there is interest in using monarch biology in eastern North America to draw inference about monarchs in western North America, we also compared density of immatures/stem in our surveys to estimates in the East.

Analytic Methods

To gain greater understanding of milkweed phenology and abundance, we fit models parallel to models of immatures/stem for counts of milkweed stems per site. For this analysis, we summed milkweed stems over all transects within a site (Table 2). Each region had 3–4 sites, and these were monitored using transects at locations where milkweed stems were dense but by counting all stems where milkweeds were sparse. We also accounted for change in sampling area in Oregon in 2018. Therefore, we expect differences among sites, simply due to the nature of sampling. We included site as a fixed effect in these analyses to account for differences in sampling effort including changes in surveys effort; we do not discuss these effects further. Analyses of milkweed stems used gaussian (normal) family distributions, because counts of stems per site were very large and approximately log-normal; use of a gaussian model also accounts for overdispersion. Counts were summed over all milkweed species, and natural log-transformed prior to analysis. Residuals of these models were approximately normally distributed (based on visual inspection for being unimodal and approximately symmetric).

To compare milkweed use by monarchs in the West to milkweed use in the East, we compare our findings to Stenoien et al. (2015), who estimated resource use by monarchs the metric of mean max eggs/stem in the Upper Midwest from 1997–2014. These data are from a project in Monarch Lab at the University of Minnesota, the Monarch Larva Monitoring Project (MLMP) which is a community science project where volunteers select sites to monitor through the breeding season.

Results and Discussion

We surveyed an average of 246.1 milkweed stems/site in 2017, and 361.3 milkweed stems/site in 2018 with a peak mid-summer (Figure 10). The difference between years was significant in most regions, but modest in magnitude (Table 4). In addition, we see similar seasonal patterns in abundance throughout the West (Figure 11).

Using a metric of maximum observed eggs/stems at each site, the density of monarch eggs per stem is substantially less in 2017 and 2018 than in the East from 1997–2014. Because the density of eggs/stem is an order of magnitude (or more) lower in the West, the analysis indicates that milkweed is potentially less limiting in the West or, if milkweed is limiting, it may only be limiting in parts of the western monarch breeding range and/or during certain times of year. The analysis also suggests that it may be critical to consider habitat attributes besides milkweed abundance when considering monarch habitat in the West, such as shade and distance to water.

Figure 10: Milkweed stems per site.

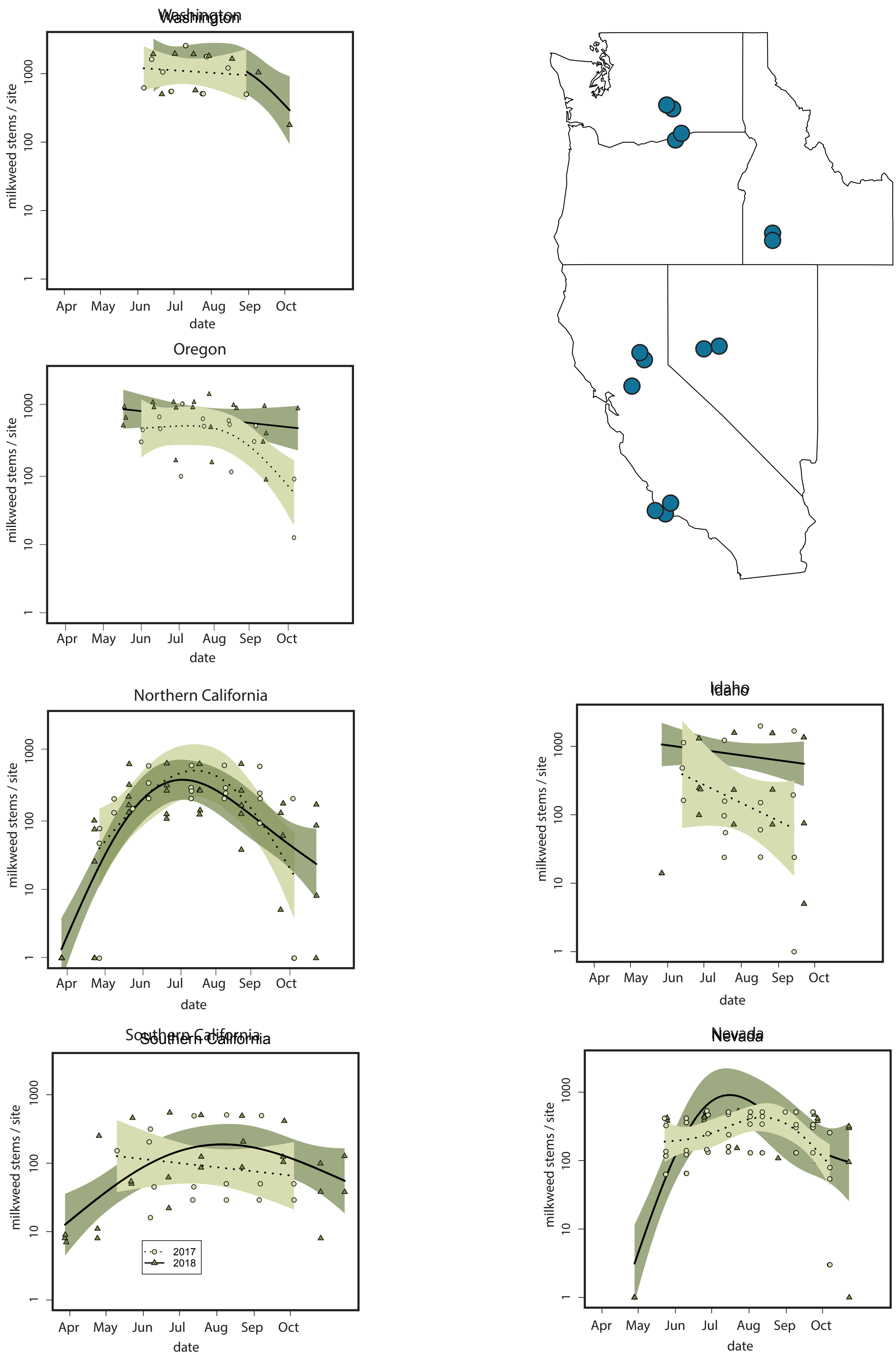
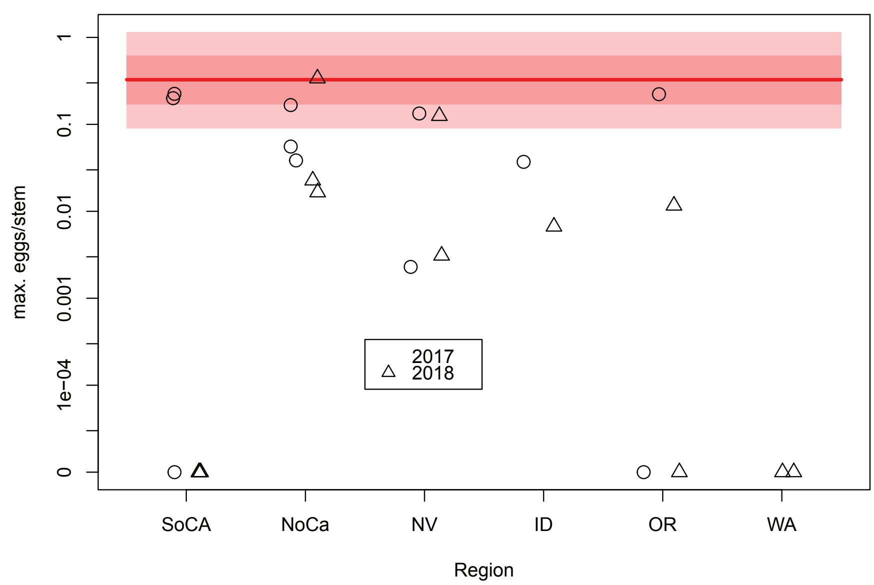


Table 4: Analysis of phenological milkweed stems per site within regions.

	Year			Day of Year (DOY)			DOY x Year		
Region	χ^2	df	P	χ^2	df	P	χ^2	df	P
Overall	2.5	1.0	0.117	142.6	2.9	<0.001	9.0	2.4	0.011
Oregon	18.6	1.2	<0.001	24.9	2.3	<0.001	18.7	2.7	<0.001
Idaho	<0.1	1.0	0.904	4.1	1.7	0.126	6.9	1.3	0.008
Nevada	<0.1	1.0	0.944	45.2	2.8	<0.001	16.0	2.4	<0.001
N. California	<0.1	1.0	0.923	65.9	2.8	<0.001	3.9	2.2	0.144
S. California	3.9	1.0	0.049	28.0	2.4	<0.001	0.2	0.9	0.618

In this project, surveyed areas were selected to maximize the likelihood we would encounter immature monarch stages. If we had, instead, randomly sampled milkweeds and surveyed those areas for immature monarchs, we expect that the egg density would have been far less than we observed. A challenge with a study with sparse breeding individuals is that if we randomly sampled milkweed stems for monarchs, it is possible we would not have detected any monarchs at all without substantially increasing the time invested in monthly sampling. Thus we expect these estimates provide an upper estimate of resource use by western monarchs in 2017 and 2018.

Figure 11: Maximum monarch eggs per stem. Red line with shaded region is mean max eggs/stem and confidence intervals estimated from Figure 4 in Stenioin et al. (2015).



3 The Population Crash

Our best estimate of western monarch population size stems from the Western Monarch Thanksgiving Count, a community science effort organized by the Xerces Society and Mia Monroe with participation by numerous dedicated volunteers. Volunteers have systematically estimated the numbers of overwintering monarchs clustered in the overwintering groves along from mid-November to early-December each season since 1997. Prior to 1997, similar counts at some sites have been done back to 1981. We used these counts to estimate the overwintering population size in the 1980s as well as the likelihood of extinction (Schultz et al. 2017). We estimated ~ 10 million monarchs wintered in these coastal groves in the 1980s. By 2016, there were fewer than 300,000 and we estimated the probability of quasi-extinction was 72% in the next 20 years. These numbers dropped to fewer than 200,000 in 2017 and plummeted to fewer than 30,000 in 2018 (Pelton et al. 2019). Thus the population crashed by greater than 80% in one season and is now at less than 99% of its historic population size.

Because climate and other conditions vary considerably from year to year, understanding breeding phenology requires surveys over multiple years to represent the range of seasonal conditions experienced by organisms. The two breeding seasons in this study, 2017 and 2018, represent stark differences between the years. The winter of 2016–17 was the first wet year after multiple years of drought across the West. Rainfall in winter 2016–2017 was intense. Across the West, rain in the 2016–2017 water-year to date is almost twice the normal rainfall. Average rainfall in Sacramento, CA from October to April is 43.2 cm and in 2016–2017 rainfall was 83.6 cm. Similarly, the average rain from April to October in Fallon, NV is 8.5 cm and in Boise, ID is 10.9 cm and in 2016–2017 it was 14.8 cm in Fallon, NV and 24.9 cm in Boise, ID. Prior to this period, because of the extreme drought, drought was a key concern relative to monarch breeding. Indeed it was a primary factor correlated with western monarch overwintering population in earlier studies (e.g., Stevens and Frey 2010). The following winter, 2017–2018, the overwintering population plummeted (Pelton et al. 2019).

We did not set up this research program to understand factors responsible for a population crash, but because we were monitoring the year prior to the crash and in the year of the crash—we can draw valuable and timely insight into western monarch biology and what might (or might not) have caused the crash. We add the caveat that large annual fluctuations in population size are an inherent aspect of butterfly—and insect—population dynamics. Factors associated with a single large drop in numbers may be different from factors responsible for long-term declines. We proceed with this analysis with the recognition that factors associated with this recent crash may or may not be consistent with long-term threats described above.

To gain greater understanding of the population crash in 2018, we consider the analyses in the sections above from the perspective of differences between 2017 and 2018, especially from the perspectives of phenology and abundance.

Milkweed

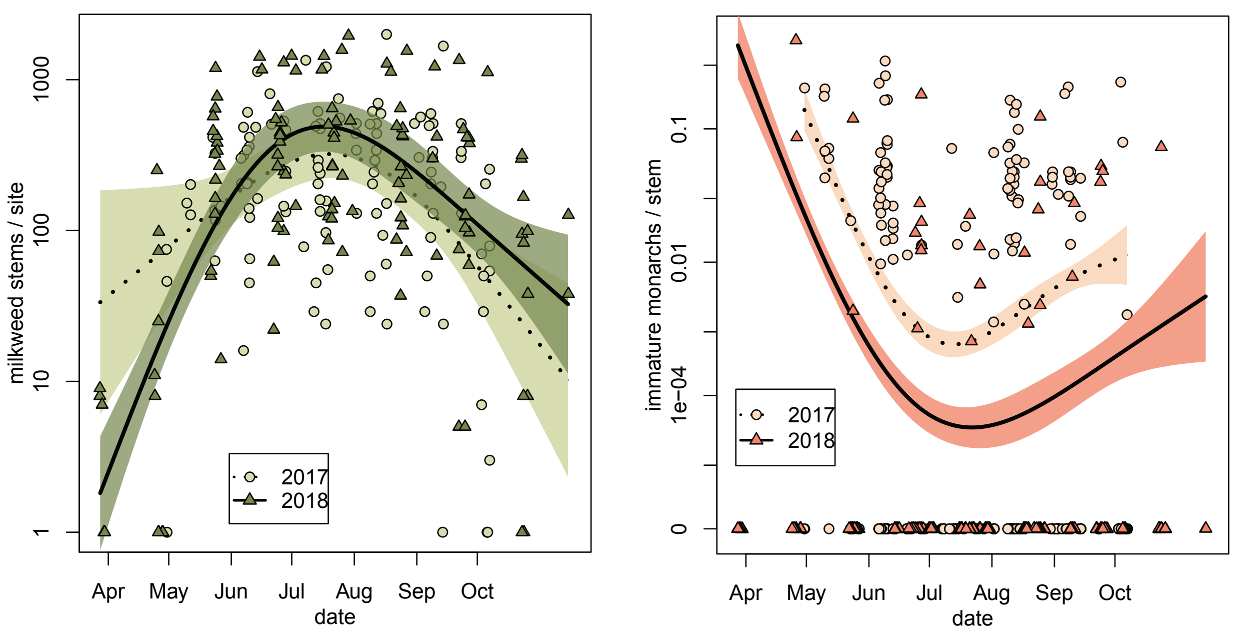
Milkweed abundance at our sites increased from 246.1 stems/site in 2017 to 361.3 stems/site in 2018, with a potential shift in abundance to earlier in the season (Table 4, Figure 12). This effect is consistent with wetter conditions in 2018 than 2017 (i.e., later end of the wet season but better conditions during drought months). This difference is reflected in a significant date_of_year x year interaction (Table 4). A key implication of these analyses is that we can rule out the hypothesis that overall resource limitation was a responsible for the 2018 crash. However, milkweed abundance was potentially less in early spring in 2018 than in 2017 and the early spring period has been identified as a potential concern in earlier studies (Espeset et al. 2016).

Monarch abundance and phenology during the breeding season

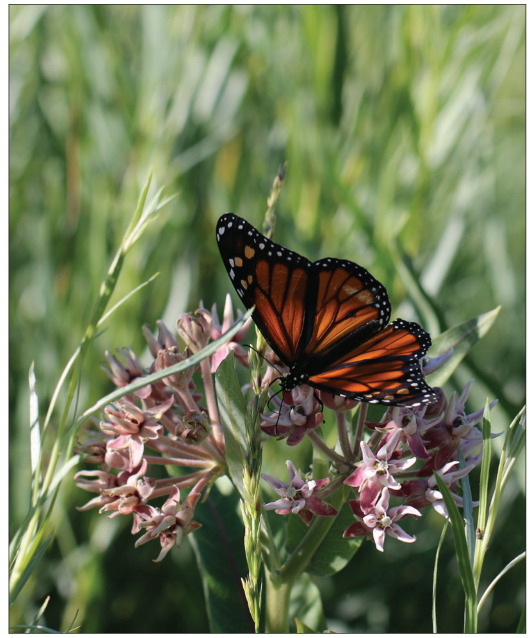
Monarchs were considerably less abundant in the breeding season 2018 than 2017 (Figure 12). In our survey areas, the average number of immature monarch butterflies per milkweed stem in 2018 was ~ 72% lower than 2017. Thus our surveys during the breeding season of 2018 mirror the crash observed by in the 2018 Thanksgiving Count results.

Moreover, our surveys reveal that monarch breeding numbers were lower in 2018 throughout the breeding season (Figure 12). That is, there was no day-of-year by year interaction (Table 1), indicating that seasonal phenology of monarchs was similar between the two year. The number of monarch immatures per milkweed stem was highest when milkweed was least abundant, especially early during the breeding season. This indicates that the 2018 crash occurred before the beginning of the breeding season. This is a critical insight to understanding the crash and we are currently investigating the additional factors related to the biology of western monarch as likely mechanisms for this crash through other research studies. Because the crash happened before the breeding season, change in abundance or management of breeding habitat throughout the range was not a focal driver of the 2018 crash. This is an important finding relative to management of breeding habitat on DoD lands. Our analyses suggest that lower survival during the winter and/or processes in early spring (February–April) may have been central to the crash, not factors during the summer breeding season. Potential processes include limitations in ability to successfully disperse to early spring breeding habitat, limitations in availability of breeding habitat in early spring or low fecundity in early spring.

FIGURE 12: MILKWEED AND MONARCH PHENOLOGY. FIGURES SHOW SEASONAL CHANGES IN MILKWEED STEM DENSITY (LEFT PANEL) AND IMMATURE MONARCH DENSITY (RIGHT PANEL) IN BOTH 2017 AND 2018, ACROSS ALL STUDY SITES.



CONCEPTUAL MODEL FOR HOW THE WESTERN MONARCH POPULATION WORKS



Monarch nectaring on milkweed. Photo: Stephanie McKnight/Xerces Society.

Overview

One goal of this project was to adapt population viability models used for eastern monarch butterflies to the ecology of western monarch butterflies. This section describes our progress in building such models, highlighting the differences we have discovered between eastern and western monarch butterflies.

For monarch butterflies in highly fragmented landscapes, the availability of milkweeds can limit population growth rates through two, fundamentally different, mechanisms. Published population models for eastern monarch butterflies (Flockhart et al. 2015, Oberhauser et al. 2017), assume that monarchs are limited by having enough food to eat – that is they assume that the ratio of monarch caterpillars to milkweed stems limits survival to pupation. This assumption means that populations are limited by density dependent survival, where density reflects the number of eggs laid per milkweed stem. In general, similar models of density-dependent host plant limitation are well established in our understanding of butterfly conservation, often leading to the implicit or explicit assumption that the number of host plants determines the carrying capacity and number of butterflies that can persist in a landscape (see, e.g., Thogmartin et al. 2017 for an example applied to eastern monarch butterflies).

Alternatively, in highly fragmented landscapes, population growth rates can be limited by the amount of time adult butterflies spend in contact with host plants (Crone and Schultz 2003, Brown and Crone 2016, Crone et al. 2019a). The assumption behind this mechanism is that butterflies at least sometimes leave habitat patches with hostplants and then need to spend time moving through unsuitable land cover types (hereafter called "matrix") to find hostplants. The time a butterfly can spend feeding and laying eggs is limited by the proportion of a butterfly's lifespan spent moving through the matrix, as opposed to in contact with host and nectar plants in suitable habitat patches. For example, during summer breeding season, an adult monarch butterfly lives ~4-6 weeks, and it is easy to imagine that butterflies who fly from spring breeding sites in northern California to southern Oregon spend at least half of this time moving through non-habitat. Furthermore, in landscapes like the Great Basin Desert in Nevada, milkweed habitat is only about 0.2% of the landscape (McKnight 2016). In these landscapes, it is easy to imagine that monarch butterflies spend only a fraction of their time in contact with milkweeds.

Contact-time limitation is density-independent, in that the breeding-season population growth rate of monarchs depends on the density of milkweeds in the landscape, as opposed to the number of monarch eggs per stem. In other words, classical density-dependent milkweed limitation determines the landscape-level carrying capacity (how many monarchs are produced by the end of the breeding season) whereas contact-time limitation determines the per capita population growth rate during breeding season.

To illustrate the contrasting predictions of the two kinds of milkweed limitation, we compiled estimates of monarch butterfly vital rates throughout the life cycle (collected mostly for eastern monarchs; Table 5) and used them to parameterize contrasting population models. We also use estimates of milkweed land cover in the Nevada (McKnight 2016) to evaluate which form of milkweed limitation is more likely to operate in the West. For classical density dependent milkweed limitation, we created a simplified (non-spatial)

Table 5: Demographic parameters used to create contrasting models with monarch butterflies limited by density dependent survival of eggs on milkweeds (DD) vs. time adults spend in contact with milkweeds (CT).

Parameter	Value	Source	Used in Model?	
			DD	CT
m, mortality per second	1.53e-6	calculated from longevity in field cages (23.25 days; (Altizer and Oberhauser 1999)), converted to survival/sec assuming 8 hours of active time/day		X
$\hat{r}$, maximum per-generation growth rate in milkweed habitat	12.1	Calculated from parameters used by Flockhart et al. 2015, adjusted for mortality in field cages (Altizer & Oberhauser 1999)	X	X
p_{max}, max. survival from egg to adult	0.7345	Flockhart et al. 2015, using larval and pupal survival data from Oberhauser 1997(Oberhauser 1997)	X	
F, lifetime eggs/female	584.5	Calculated from parameters used by Flockhart et al. 2015, adjusted for mortality in field cages (Altizer & Oberhauser 1999)	X	
β_0 & β_1, slope and intercept of density-dependent survival	1.0175 -0.1972	(Flockhart et al. 2012)	X	
$\bar{z}$, pref at patch edges	0.33	calculated from data in Zalucki and Kitching (1982)		X
D_1, movement in habitat (m2/sec)	0.44	calculated from data in Zalucki & Kitching (1982)		X
D_2, movement in matrix (m2/sec)	10,000	Equivalent to ~ 6 km/hr and ~ 17 km/day; see Davis 2017		X

version of the model used by Flockhart et al (2015) for eastern monarch population viability analysis. For contact-time implementation, we used spatially implicit integrodifference equation models (Musgrave and Lutscher 2014, Lutscher and Musgrave 2017, Crone et al. 2019a), which calculate population growth rates as a function of vital rates (adult and larval survival, and adult fecundity), adult movement (movement rates in habitat and matrix, and preference for remaining in habitat at patch interfaces), and landscape (defined by the proportion of the landscape composed of habitat vs. matrix land cover types).

Milkweed limitation through density-dependent survival of immatures (DD)

Following Flockhart et al. (2015), the core of this model is a density dependent survival function of monarch immatures, based on experiments conducted by Flockhart et al. (2012). We simplified the monthly growth rates in Flockhart et al. (2015) to calculate a per-generation population growth rate of monarch butterflies, leading to the following equation:

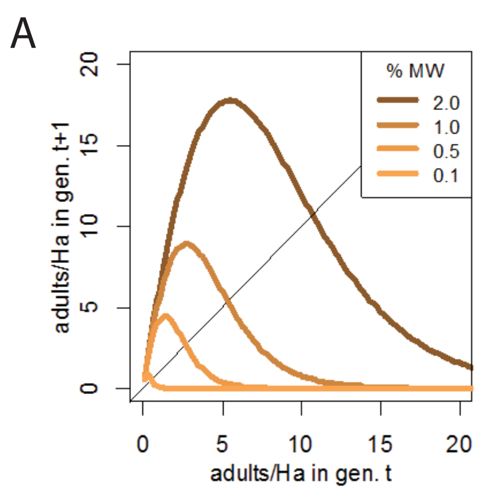
$$N_{t+1} = N_t\hat{r}\frac{p_{max}}{1+\frac{1}{\exp(\beta_0-\beta_1\frac{0.5FN_t}{M})}} \qquad \text{eq. 1}$$

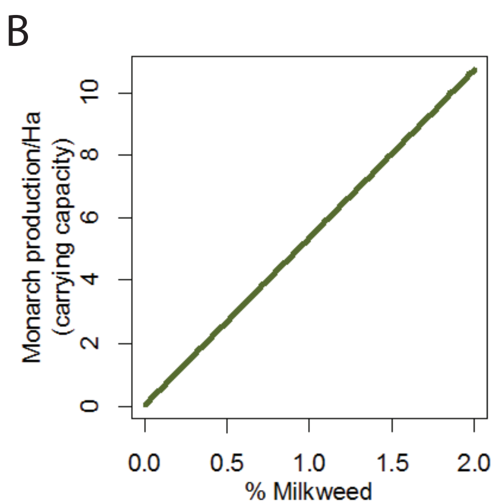
In this equation, N_t is the number of monarch butterflies / Ha in generation *t*, *M* is the number of milkweed plants per Ha on the landscape, and all other variables are demographic parameters defined in Table 5. As a first approximation for comparison with contact-time limitation models (below), we calculated % milkweed at landscape scales assuming one milkweed stem = 1 m^2 of land cover.

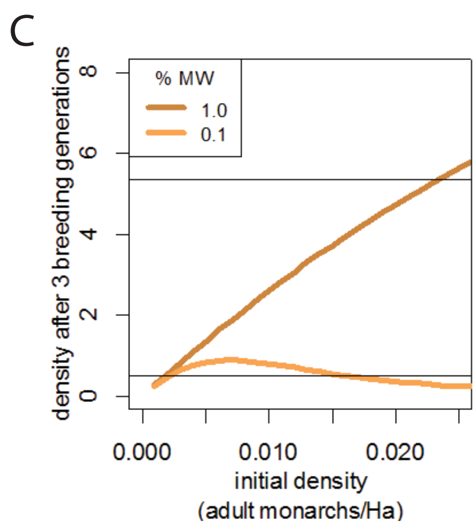
This model predicts that populations will grow to a carrying capacity determined by the density of milkweeds on the landscape (Figure 13 A & B). This model was originally developed for eastern (not western) monarch butterfly populations. Monarch butterflies have ~3 breeding generations in the upper Midwest of the United States (Oberhauser et al. 2017) -the North Central region in Figure 1). Monarch butterflies are predicted to reach their carrying capacity within three generations, as long as the starting density of butterflies in the first generation that reaches the north central United States is at least 0.4% (1/20) of the carrying capacity (Figure 13 C).

Figure 13. Predictions from density-dependent survival models for monarch butterflies.

(A) Recruitment curves, i.e., the number of predicted butterflies in one breeding generation, depending on the number in the previous generation. (B) Carrying capacity as a function of % milkweed on the landscape. (C) Abundance of monarch butterflies after 3 generations of breeding, when starting densities are very low. Thin black line indicates carrying capacity.







Milkweed limitation through contact-time limitation of adult butterflies and milkweeds (CT)

Musgrave and Lutscher (2015) showed that, in heterogeneous landscapes composed of habitat patches and a non-habitat matrix, a species population growth rate can be calculated by solving the following equation for the per-generation growth rate, λ_{CT}

$$\frac{\overline{-\left(\frac{1}{\lambda_{CT}}\hat{r}-1\right)}\, l_1}{2}\Bigg) = \frac{\bar{z}\sqrt{\frac{m}{D_2}}}{\sqrt{\left(\frac{m}{D_1}\frac{1}{\lambda_{CT}}\hat{r}-1\right)}}\sqrt{\frac{D_2}{D_1}}\tanh\left(\frac{\sqrt{\frac{m}{D_2}}\, l_2}{2}\right) \qquad \text{eq. 2}$$

This model can be solved analytically because it makes the specific assumption that landscapes can be approximated by parallel strips of habitat and matrix land covers (Fig 14a). In this equation, l_1 is the width of habitat strips and l_2 is the width of nonhabitat strips, making $\frac{l_1}{(l_1+l_2)}$ equal to the proportion of habitat on the landscape, and $100 \times \frac{l_1}{(l_1+l_2)}$ equal to the % milkweed habitat at landscape scales when this equation is applied to monarch butterflies. [This assumption is obviously an approximation of real landscape complexity but is useful as a first cut because it does not require creation of complex simulation models. It is also a useful starting point when landscape structure is potentially variable, or unknown.] Tan and tanh are the familiar tangent and (less familiar) hyperbolic tangent functions, respectively. All other variables are as defined in Table 5. This equation represents Musgrave and Lutscher's case S, as presented in their equations 55 and 57 (Musgrave and Lutscher 2014), modified to exclude permanent settling of adult butterflies in habitat patches, as in Appendix S4 of Crone et al. (2019).

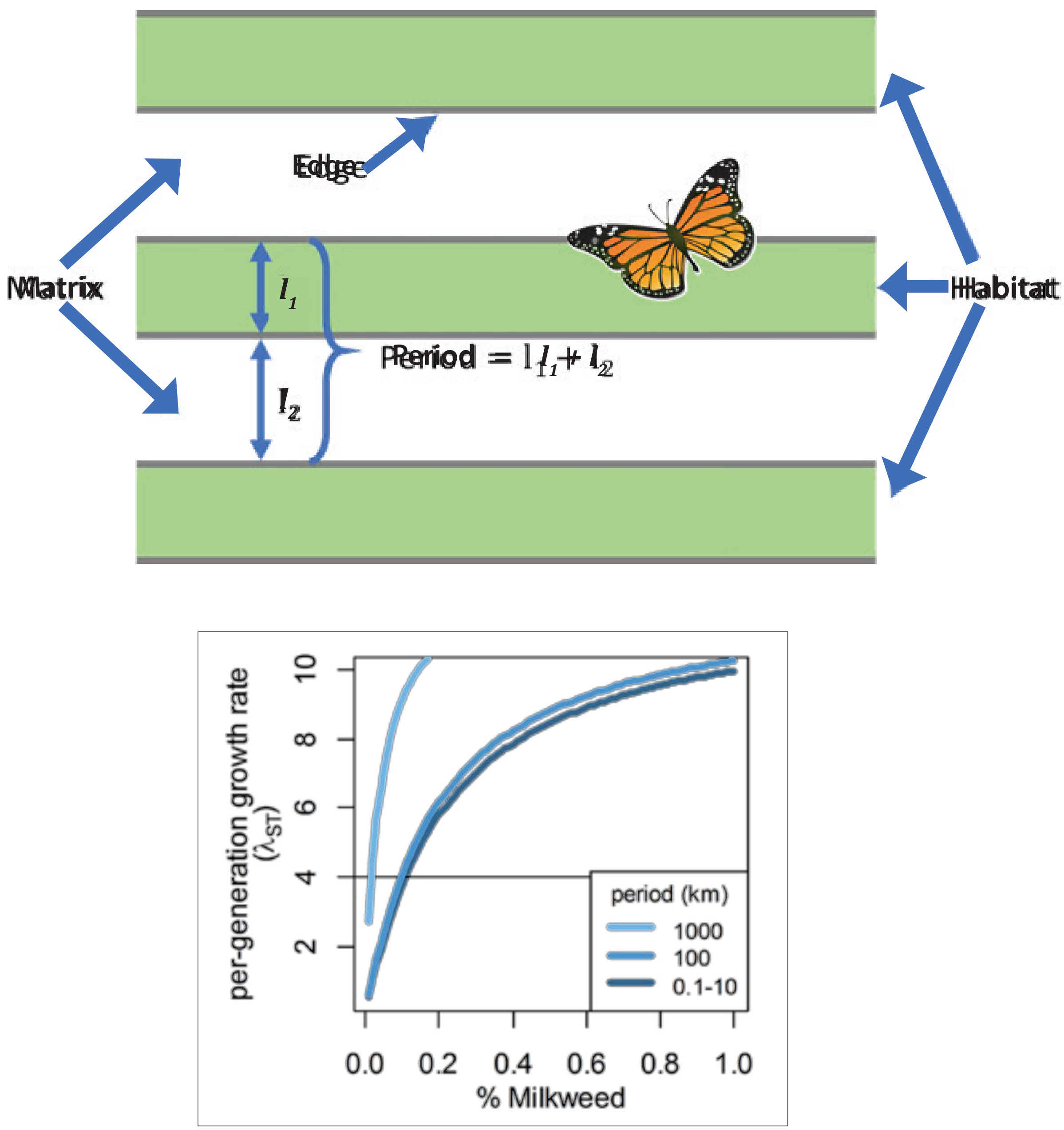
For the parameters in Table 5, this model predicts that monarch butterfly populations will grow during the breeding season (i.e., $\lambda_{CT} > 1$) if milkweed cover is > 0.02% (Figure 14b). However, for populations to persist, monarch butterflies need to not only grow during breeding season, but grow enough to make up for high mortality during migration and overwintering. We also want monarch butterfly populations to expand fast enough to fill the western states, e.g., in order to use available milkweed habitat in Washington, Oregon and Idaho. We estimate that populations probably need to increase four-fold per breeding generation in order to meet these criteria (E. Crone, unpubl. calculations). For these parameter values, the minimum cover for monarch butterfly populations to persist (i.e., for $\lambda_{CT} > 4$) is 0.11%. At very high milkweed cover, population growth rates reach the maximum value of $\hat{r}$ = 12.1; in these cases, dynamics would presumably be limited by density dependence, not contact time. For parameters in Table 5, and a 1-km period landscape, growth rates approach their maximum at about 5-15% milkweed cover ($\lambda_{CT} > 8$, 10, and 12 at ~ 0.5%, 1% and 17% cover, respectively, calculated using eq. 2).

Contrasting predictions of density-dependent vs. contact-time milkweed limitation

To further illustrate the contrast between density-dependent and contact-time milkweed limitation, we used both models to predict the consequences of a shift from 0.11% milkweed cover to 0.1% milkweed cover during the breeding season. We chose this change because it illustrates the contrasting predictions of the two models. The particular quantitative predictions of both models depend on the parameter estimates, and we emphasize that these are poorly known, and often estimated from only one or two locations in the range

Figure 14. Upper panel: Cartoon of stylized landscape used in the contact-time limitation (CT) model. Figure modified from Crone et al. 2019.

Lower panel: Predicted per-generation monarch butterfly growth rates when populations are contact-time (CT) limited. Landscape period refers to the spatial grain of the habitat, e.g., in landscapes with a 10 km period, and 1% milkweed, milkweed patches are approximately 100 meters wide (10,000 meters x 0.01 = 100 meters), and in landscapes with a 1 km period and 0.1% milkweed, patches are approximately 1 meter wide (1,000 meters x 0.001 = 1 meter). Model predictions do not depend strongly on landscape period, over realistic values of 0.1-100 km periods. At very high periods (1000 km), monarch populations could persist at very low milkweed cover values, but these would be isolated populations, not a population that could expand through the landscapes (i.e., habitat gaps of ~ 1000 km would be too far for populations to cross).



of monarch butterflies worldwide; parameter estimates in Table 5 come from the eastern US and Australia, and none have been measured for western monarchs. Further research would be invaluable for using the models to guide conservation, especially measuring movement and vital rates for monarch butterflies to guide conservation in the west. Nonetheless, the qualitative differences caused by the core assumptions of each model do not depend on the parameter estimates, in the sense that they would show the same patterns, even if they occur at different habitat thresholds.

Specifically, simulated a situation in which milkweed cover was 0.11% for five years, then dropped to 0.1% for ten years, then was restored to 0.11%. For the density-dependent model, we assumed that populations were large enough to reach their carrying capacity during breeding season. Therefore, the density-dependent model predicted that populations would grow to the carrying capacity associated with milkweed cover in each year (Figure 15 A-C), including immediately returning to their original abundance after habitat was restored. For the contact-time limitation model, we predicted annual population growth rates using

$$\lambda = s_F s_O (\lambda_\phi) {\lambda_{CT}}^3 \qquad \text{eq. 3}$$

where λ is the annual population growth rate, λ_{CT} is the per-generation breeding season growth rate (calculated using the contact-time limitation model described above), and all other parameters are as defined in Table 6. Using these parameters, the predicted annual population growth rate was 1.05 with 0.11% milkweed, and 0.81 with 0.1% milkweed (Figure 15 D-F). Therefore, the population increased during years with 0.11% milkweed, and declined during years with 0.1% milkweed. However, the declines were noticeably sharper than the increase (Figure 15 E). Therefore, the contact-time limitation model predicted that populations would not recover to their original abundance, even 10 years after milkweed was restored to its original level (Figure 15 F). This effect is partly due to the asymmetry in the change in growth rates. However, even if the changes were perfectly symmetric, it would take as many years for the population to recover after habitat restoration as the number of years it had experienced of habitat loss.

Table 6: Additional parameters used to estimate annual population growth rates for monarch butterfly populations limited by contact time with milkweeds (CT model).

Parameter	Value	Source
s_o, survival during overwintering	0.30	Pelton et al. (2019)
s_o, proportion surviving fall migration	0.05	Estimated from sighting and resighting rates of monarch butterflies in James et al. (2018)
ϕ, adjustment for lower reproduction monarchs in the overwintering generation*	0.43	Thomas, Crone & Schultz, unpubl. data

* Per-generation growth rates for monarchs in the generation that overwintered were calculated by substituting $\phi\hat{r}$ for $\hat{r}$ in eq. (2). This growth rate is λ_ϕ in eq. (3).

Figure 15 A-C. Effects of shift from 0.11 to 0.10% milkweed with density dependent milkweed limitation.

A B C

$N^* = 0.59$ $N^* = 0.59$

$N^* = 0.54$

Figure 15 D-F. Effects of shift from 0.11 to 0.10% milkweed with contact time limitation.

D E F

$\lambda = 1.05$ $\lambda = 1.05$

$\lambda = 0.81$

Which model is better for western monarchs?

Based on our experience working with western monarch butterflies, we believe contact time limitation is the appropriate framework for evaluating western monarch population viability.

This reasoning comes from two sources:

First, the limited data we have available suggests low milkweed cover and highly fragmented landscapes. The only quantitative landscape-scale estimate of western milkweed cover is 0.2% on public lands in Nevada (McKnight 2016). We suspect cover is substantially lower at key pinch points in the western range, especially the Central Valley of California, which is intensively managed for agriculture. If we were confident that the parameters in Table 5 are appropriate for western monarchs, we could use milkweed cover estimates to evaluate whether monarch butterflies are likely to grow to carrying capacity in the west (similar to the example calculations shown above). However, we strongly recommend interpreting these numbers with caution until we measure monarch butterfly vital rates, movement parameters, and milkweed cover in the western states, which (with the exception of McKnight 2016) has not yet been done.

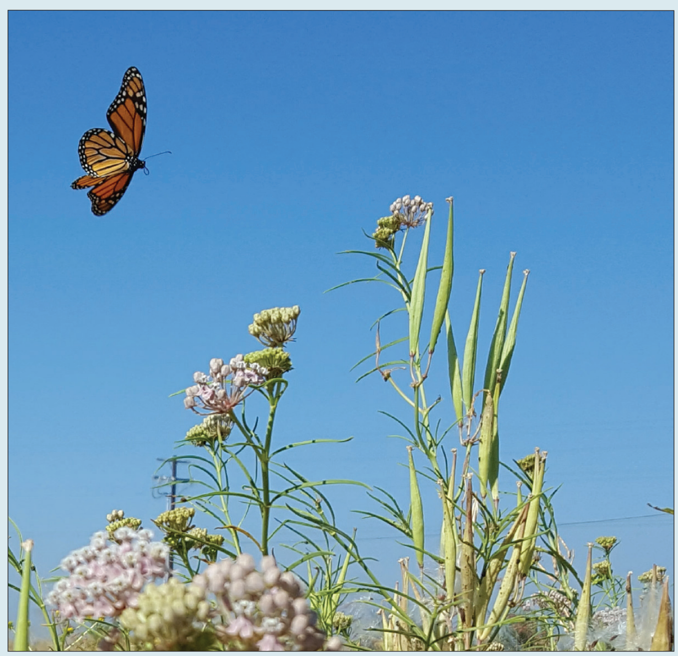
Second, during the field surveys we conducted as part of this project, we observed vastly lower densities of monarch eggs and larvae per stem than have been reported for eastern monarch butterflies (see Section 2 in this report). Many areas had thousands of stems of milkweed and no monarchs at all. It is difficult to believe that ratios of monarchs to milkweed stems *per se* limit monarch survival. In spite of locally abundant milkweed, however, we often had to search extensively in the landscape to find milkweed patches (especially in the Central Valley of California). This experience is also consistent with the idea that monarch fecundity could be search-time limited.

Of course, these analyses are only the beginning of population viability models for western monarch butterflies. More extensive tests of the mechanisms behind milkweed limitation would be a valuable area for future research, in order to understand how milkweeds limit monarchs, how to target habitat restoration, and how to set appropriate targets for management and recovery of monarch butterfly habitat in the west.

SUMMARY

In summary, one key difference between the **density-dependent** and **contact-time** limited population models is how they respond to **habitat loss** and **restoration**. In the presence of density dependent milkweed limitation, the amount of milkweed on the landscape sets a carrying capacity, and the monarch butterfly population quickly grows to this carrying capacity. Monarch butterfly abundance quickly matches available habitat.

In the presence of contact time limitation, monarch butterfly population growth rates are affected by milkweed abundance. This means that populations might continue to decline after habitat destruction stops, if habitat destruction causes the annual growth rate to be less than one. Furthermore, the relationship between milkweed abundance and population growth rates is nonlinear (Figure 15), which means that, under some conditions, small changes in milkweed abundance lead to large changes in population growth rates and that population recovery following restoration will take time.



A monarch flies over *Asclepias fascicularis* (narrowleaf milkweed). Photo: Stephanie McKnight/Xerces Society.

Monarch larva on *Asclepias incarnata* (swamp milkweed). Photo: Stephanie McKnight/Xerces Society.

CONCLUSIONS AND BENEFITS TO DEPARTMENT OF DEFENSE

When a species occurring on military lands is listed under the Endangered Species Act, military training and operations can be negatively impacted. Should the monarch be listed, the impact to military training operations could be especially extensive, given the broad distribution of monarchs in the US. This project includes installations across 5 large western states with benefits to DoD lands across the western US. This knowledge benefits the military mission by allowing managers to balance habitat protection with training activities. Developing and implementing proactive conservation strategies before the species becomes federally listed increases the probability that USFWS may find that listing this species is not warranted. Further, if a species which has had proactive management as a candidate does get listed, regulatory constraints placed on activities at the base are substantially reduced if the base has been proactive. To date, we see several specific benefits to DoD from this research program.

First, this research identifies timing within the monarch annual cycle most likely associated with recent large amplitude swings. That is, in 2017 and 2018, our research indicates that the late wintering season and/or early spring breeding season is the timing likely associated with the dramatic crash in the population. This is critically important because it means this rapid drop from 2017 to 2018 was not directly caused by habitat management across much of the breeding range, which is the dominant habitat type we surveyed during this project. This indicates that installation management in monarch breeding areas were not a dominant driver of this recent acute decline.

Second, if a species such as monarch with a broad use of a large landscape is protected under the Endangered Species Act, a monitoring program such as this provides vital information about times during the life cycle that contribute to sharp drops and times that were less likely to make large contributions. This information provides vital flexibility to installation resource managers in responding to species' needs. Continuation of a program such as this can provide vital information to installation managers into the future. Although the surveys on the ground are relatively sparse (a few days per month in each of several broad regions), together they can highlight key processes in the population. Moreover, it provides insurance going forward that outside influences cannot point to installation resource management as a dominant contributor to population declines.

Third, this research indicates that broad-scale milkweed limitation was not the proximate cause of the 2018 crash. Our analyses indicate that milkweed did not dramatically decline from 2017 to 2018 (Figure 12). It is important to note that use of milkweed by monarchs, as measured by eggs/milkweed stem is orders of magnitude lower across the West than in the eastern population (Figure 9). If milkweed or resources are limiting to western monarch, it requires much finer/local scale assessments to consider factors such as seasonal timing, regional availability, milkweed species diversity, and other aspects of habitat structure such as nectar, shade or distance to water. That is milkweed limitation may be critical at key times of year or in key regions, but not as a broad and overarching factor across the entire breeding range. This is of great benefit to installation resource managers because it suggests that at many installations, milkweed enhancement is not likely to be the sole focus of monarch restoration or enhancement efforts if monarchs are protected under the ESA

Fourth, this research provides specific recommendations for installation managers to enhance habitat value for breeding monarchs and provide contributions to this emblematic species. We developed *Monarch Conservation on Department of Defense Lands in the West: Best Management Practices*, including installations specific guidance for INRMPs. These recommendations are aimed at balancing training needs at each installation with resource needs by monarch butterflies.

Fifth, this research advances our understanding of monarch milkweed use. That is, milkweed use by monarchs varies by species and regions varies and from year to year. Based on our analyses, increasing milkweed species diversity is important to increase the phenological window that milkweed is available for monarchs' use. This will buffer the population given variation in seasonal swings in temperatures and precipitation.

Finally, our modeling work demonstrates that population increases or declines do not necessarily mean that the breeding habitat is getting worse. Although breeding habitat does not appear to be associated with the 2018 crash, habitat limitations at key times during the annual cycle and/or in key locations within the spatial distribution may play a key role in driving long-term declines in monarch abundance in the west. Habitat management and restoration to increase contact rates between milkweed and monarchs could be essential to allowing the monarch population to increase from its currently small population size. Such efforts on and off of DoD lands may be important to range wide persistence of western monarch.

Understanding monarch habitat use on DoD installations is crucial to maximizing proactive management for monarchs while minimizing interruption of operations. Continued and future programs such as this provide a basis for tailoring management to ecosystem and species needs in balance with mission of installations for DoD use of the lands.

Monarch larva on milkweed. Photo: Stephanie McKnight/Xerces Society.

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