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The changing landscape of urban monarch butterflies: Patterns in milkweed species composition, winter vegetation and breeding, and larval predation in the eastern San Francisco Bay Area

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The changing landscape of urban monarch butterflies: Patterns in milkweed species composition, winter vegetation and breeding, and larval predation in the eastern San Francisco Bay Area

By

Leslie Ann McGinnis

A dissertation submitted in partial satisfaction of the

requirements for the degree of

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in the

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of the

University of California, Berkeley

Committee in charge:

Professor George Roderick, chair
Professor Nicholas Mills
Professor Timothy Bowles

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Abstract

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As overwintering western monarch butterfly (*Danaus plexippus* (L.)) numbers have decreased, conservation groups have urged agencies and private citizens to plant milkweed to support monarch larvae. However, demand for native milkweed plants has outpaced availability in nurseries and seed companies, especially in the western United States. Gardeners have planted the milkweed that they could obtain, often resulting in large numbers of non-native milkweeds in residential gardens. In Chapter 1, I conducted a survey of a set of neighborhoods in the eastern portion of the San Francisco Bay Area of California to understand changes in the prevalence, species composition, and spatial distribution of milkweeds planted by gardeners in an urban matrix. These neighborhoods are adjacent to two monarch overwintering sites and have hosted winter breeding monarchs in recent years. To understand the changing milkweed landscape, I surveyed gardens from October 1 to November 24, 2020, and resurveyed the same parcels from October 14 to November 30 of 2022. I recorded the presence or absence of milkweed plants in the genus *Asclepias* and in related genera *Gomphocarpus* and *Oxypetalum* in each garden, along with detailed information about all milkweed plants and monarch larvae observed. Milkweed gardening expanded over the two-year period with a higher percentage of gardens containing milkweed in 2022 versus 2020. Only four species of milkweeds were regularly found in gardens. More gardens contained native milkweeds in 2022, with the percentage of milkweed-containing gardens with *Asclepias fascicularis* and *Asclepias speciosa* both increasing by 4.5 percentage points over the two years. Many gardens still contained non-native milkweeds in 2022. The percentage of milkweed growing gardens with *Asclepias curassavica* decreased by 4.8 percentage points, but the percentage growing *Gomphocarpus physocarpus* increased by 7.3 percentage points. These patterns likely reflect the changing availability of native milkweeds and lack of clarity surrounding outreach about non-native milkweeds. For Chapter 2, I documented the winter availability of milkweeds in the same region during the winter of 2020-2021. I re-visited gardens identified during the fall of 2020 and followed how milkweed plants were maintained throughout the winter. After recording if non-native milkweeds were cut back during the winter, I classified the degree of pruning and recorded the presence or absence of monarch larvae. Additionally, I conducted more detailed counts of larvae and eggs on select plants. For gardens containing non-native milkweeds, I

found that approximately 18% of such gardens are well pruned close to the ground leaving little to no vegetation, an additional 15% have plants that are partially pruned, and approximately 67% appear to not be pruned at all. Monarch adults, larvae, and eggs are present in local gardens throughout the duration of the winter but are less common in late January through mid-February. Many larvae present in the first two weeks of January 2021 were fourth and fifth instar larvae remaining from the previous year. Large concentrations of eggs became common in early March of 2021, with high egg densities on many plants. While non-native milkweeds were available to and used by monarchs during winter months, some native *Asclepias fascicularis* and *Asclepias speciosa* plants retained green vegetation into mid-January of 2021, calling into question the assumption that all native milkweeds die back during the winter. In Chapter 3, I documented common predators of monarch larvae in urban gardens in the San Francisco Bay Area. From the summer of 2021 through the fall of 2024, I recorded all observed fatalities of monarch larvae in a set of experimental gardens. I also conducted structured predation trials from August through mid-October of 2023. Almost all documented monarch fatalities were caused by predation by invasive *Polistes dominula* wasps. During extended day and nighttime observations, I observed two species of vertebrate predators consuming monarch larvae: a scrub jay (*Aphelocoma californica*) and a dusky-footed wood rat (*Neotoma fuscipes*). Other species documented attacking or consuming monarch larvae were a yellow sac spider (*Cheiracanthium* spp.), Argentine ants (*Linepithema humile*), and yellow-jackets (*Vespula pensylvanica*). Attacks by *Polistes dominula* wasps would sometimes result in monarch larvae dropping from plants and escaping into dense ground cover or weedy vegetation around plants. However, most attacks were fatal and resulted in larvae being skinned, gutted, and dismembered and delivered to wasp nests with repeated trips until only gut matter and head capsules remained. High fatality days generally occurred on hot days in the late summer. Attacks were almost always mounted by a single wasp that had encountered the plant. In earlier summer trials, attacks were less common on monarch larvae in two gardens dominated by agricultural plants despite the wasps being ubiquitous in those gardens. *Polistes dominula* on these days could often be seen hunting along crops in the Brassicaceae, potentially searching for lepidopteran larvae of other species. My study provides important data on habitat used by both larval and adult monarchs for a poorly understood portion of the western monarch butterfly population. My study also provides an example of ways to conduct science that are place-based and conducted by researchers who are part of the regional community. Conservation practitioners should consider the future impact of rising temperatures on the growth of all species of milkweed. Future efforts should also focus on control of *Polistes dominula* wasps and working with gardeners to locate wasp nests early each season.

DEDICATION

I dedicate this dissertation to my mother, Gail Joanne Tupper McGinnis. I miss you every day. Completing this degree has been a battle and I wish that you could have lived to have seen me finish. Thank-you for teaching me my love of gardening. I think about you every time I pick a seed pod on the side of the road and every time a monarch or tiger swallowtail flies above me.

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Chapter 1: The changing patterns of the urban milkweed landscape: A case study of prevalence, species composition, and distribution of milkweed gardens in the East Bay

ABSTRACT

As overwintering monarch butterfly (*Danaus plexippus* (L.)) numbers have decreased, conservation groups have urged agencies and private citizens to plant milkweed to support monarch larvae. Demand for native milkweed plants has outpaced availability in nurseries and seed companies, especially in the western United States. Gardeners have planted the milkweed that they could obtain, only to be told that they should be planting some species of milkweed and not others. Some counties have also banned the sale of one milkweed species. The impacts of these changing conservation messages and changing availability of milkweeds on actual gardens is poorly understood. To understand changes in the prevalence, species composition, and spatial distribution of milkweeds planted by gardeners in an urban matrix, I conducted a survey of a set of neighborhoods in the eastern portion of the San Francisco Bay Area of California. These neighborhoods are adjacent to two monarch overwintering sites and have hosted winter breeding monarchs in recent years. The dynamics of these urban monarchs have been mostly understood from anecdotal accounts of gardeners. Research interest in this population of monarchs increased after the record low count of western monarchs in the winter of 2020-2021, however little formally collected data exists before that point. I surveyed 2256 land parcels representing gardens from October 1 to November 24, 2020, and resurveyed the same parcels from October 14 to November 30 of 2022. I recorded the presence or absence of milkweed plants in the genus *Asclepias* and in related genera *Gomphocarpus* and *Oxypetalum* in each garden. For gardens with milkweeds, I recorded the species present, the number and size of plants, the general health of plants, and if the plants were located in green strips or front yards. Additionally, I took voucher photos of all plants for comparison over time and recorded if larvae were readily visible. I identified 90 gardens growing milkweeds in 2020 and 127 growing milkweeds in 2022 in the same area. Milkweed gardening expanded over the two-year period with a higher percentage of gardens containing milkweed in 2022 versus 2020. Only four species of milkweeds were regularly found in gardens. More gardens contained native milkweeds in 2022, with the percentage of milkweed-containing gardens with *Asclepias fascicularis* and *Asclepias speciosa* both increasing by 4.5 percentage points over the two years. Many gardens still contained non-native milkweeds in 2022. The percentage of milkweed growing gardens with *Asclepias curassavica* decreased by 4.8 percentage points, but the percentage growing *Gomphocarpus physocarpus* increased by 7.3 percentage points. These patterns likely reflect the changing availability of native milkweeds and lack of clarity surrounding outreach about non-native milkweeds. My study provides important data on habitat used by both larval and adult monarchs for a poorly understood portion of the western monarch butterfly population. My study also provides an example of ways to conduct science that are place-based and conducted by researchers who are part of the regional community.

INTRODUCTION

As the world settles more firmly into the Anthropocene and the impacts of global change become more evident to the general population, scientists must carefully consider conservation policies. Humanity has altered species ranges through trade and travel, changing species assemblages throughout the world. Restoration practitioners must ask themselves "What is natural?" and what historical timepoint should they consider as a restoration goal. The answers to these questions may differ greatly between scientists, conservationists, and the general public.

Monarch butterflies provide a unique case study to analyze how both scientists and the public approach conservation and define what is natural. These iconic butterflies grew in fame after the overwintering colonies in the mountains of Michoacan, Mexico were described by scientists in the mid-1970s (Urquhart 1976). Written records of monarchs overwintering in Costal California date back to 1880 (Bush 1881; Lane 1993; Thaxter 1880; Vane-Wright 1993). While migratory monarchs are thought of as pre-dating anthropogenic disturbance in conservation discourse, scientists have long suggested that the phenomenon is a relatively recent response to colonial deforestation and conversion of land to disturbed prairie habitat favoring milkweed plants (Vane-Wright 1993). This hypothesis has been recently supported after advances in genomic and machine-learning methods (Boyle *et al.* 2023). North American monarchs and milkweeds experienced population expansions both between 10,000-20,000 and 200 years ago likely originating from from South America (Boyle *et al.* 2023; Vane-Wright 1993). Monarchs may have also benefited from pre-colonial indigenous land management practices which may have promoted grassland habitat supportive of *Asclepias* species (Denevan 1992). Monarchs are also distributed throughout the Caribbean islands, Central America, and parts of northern South America (Malcolm 2018). Human introduction of milkweeds also facilitated monarchs expanding to Australia, New Zealand, Hawaii, Samoa, Fiji, and New Caledonia in the 1800s (Vane-Wright 1993). More recently, monarchs have colonized parts of Spain, Portugal, Morocco, and the Canary Islands (Fernandez-Haeger *et al.* 2015; Malcolm 2018). Despite their relatively recent origin in many regions, monarchs and their migratory patterns are loved throughout society and their recent declines have resulted in a surge of research and public mobilization.

Overwintering aggregations of monarchs have decreased dramatically over the past 40 years, with some yearly counts showing extreme year-to-year variation (Jepsen & Black 2015; Malcolm 2018). These decreases have been seen in both the eastern monarch population and the western monarch population (Schultz *et al.* 2017). Monarch scientists and enthusiasts can generally agree on a long list of threats to monarch butterflies, but the severity and relative contribution of each threat is still a subject of debate. Threats include loss of milkweed, loss of nectar resources, degradation of overwintering habitat, climate change, invasive pests and plants, habitat fragmentation, and culture of monarchs and invasive milkweeds (Jepsen & Black 2015; Malcolm 2018). Monarch larvae can be killed by *Bt* (*Bacillus thuringiensis*) expressed by GMO crops (Losey *et al.* 1999) and by fertilizers, herbicides, and pesticides (Halsch *et al.* 2020, 2022). Loss and change of floral resources can impact monarch's lipid storage (Brower *et al.* 2015). Climate change including increased temperatures, plant drought stress, and elevated carbon dioxide can also change the chemistry of plants used for both larval and floral resources (Brower *et al.* 2015; Decker *et al.* 2018; Decker & Hunter 2020; Faldyn *et al.* 2018). With such a complex and daunting list of threats, simply planting milkweed can be a way for an average person to contribute while also learning about monarch ecology.

Recent years have seen a dramatic expansion in cultivation of milkweeds to attract and support monarch butterflies. As more agencies and private gardeners have sought out milkweed plants, the demand has outpaced the commercial availability of both plants and seeds (Borders & Lee-Mäder 2014; Borders & Mader 2011). Milkweeds had a long history of being banned as noxious weeds in municipalities throughout the United States (Falck 2002; Redick 2014). Native plant gardeners could be cited and have their gardens ripped out due to these antiquated laws (Redick 2014). It is not surprising that native milkweeds were not widely available in commercial nurseries. Additionally, as with many native plant species, many native milkweeds require specialized germination treatments which can vary within species between populations (Bandara *et al.* 2019; Kaye *et al.* 2018; Landis 2014; Landis & Dumroese 2015). Some milkweed species require soil amendments and can take several years to become established and flower from seed (Borders & Lee-Mäder 2014; Landis & Dumroese 2015). Rhizome divisions are typically done during winter dormancy (Landis & Dumroese 2015), limiting the time frame during which a producer could expand their crop and resulting in spring shipments of plants being dormant or in visibly poor condition (personal observations). A more well-established milkweed industry has existed in the central mid-western United States, but even suppliers in that region can experience shortages (Borders & Lee-Mäder 2014). While well-intentioned, the milkweed planting movement did not adequately consider nursery availability, shortages of plants and seeds, the diversity of plants used, or the ubiquity of pesticides in nurseries. Pesticide contamination has been shown to be high in many plants purchased from nurseries (Halsch *et al.* 2020, 2022). Nurseries sold what they could produce and sell and gardeners purchased and planted the plants that were available to them. The result has been met with mixed enthusiasm.

As milkweed gardening has grown in popularity, the conservation recommendations given to gardeners have changed. Agencies have specifically recommended only planting native milkweeds. Conservation groups have expressed concerns over tropical milkweed impacting disease prevalence and disrupting migratory patterns of adult monarchs (Satterfield *et al.* 2016). One study found that monarch larvae reared on tropical milkweed *Asclepias curassavica* had higher survival to adulthood and mass than larvae reared on *Asclepias incarnata* (native in the eastern United States, but not in California) (Faldyn *et al.* 2018). However, this pattern changed when larvae and plants were grown under elevated temperatures simulating future climate change. Under elevated temperatures, monarchs reared on *A. curassavica* fared worse as plant cardenolide levels increased (Faldyn *et al.* 2018). Lobbying efforts resulted in officials in Marin County, California banning the sale of *Asclepias curassavica*, only one of the non-native milkweeds. One prominent lepidopterist summarized the legislation as "hogwash" (Garvey 2022). Messaging against non-native milkweeds has ranged from recommending that gardeners cut back their non-native milkweeds in winter, sometimes specifying to do so in October, to recommending that non-native milkweeds be removed altogether. Gardeners have responded with confusion and frustration, questioning the logic behind recommendations (personal communication). Some residential gardeners in the San Francisco Bay Area have even reported pressure from strangers to remove their non-native milkweed on private property. Given the mixture of messages to the public, it is important to understand what is actually happening in urban and suburban residential settings and if and how patterns are changing. How common is milkweed gardening? Which species of milkweeds do gardeners grow? Are these gardening practices changing over time? Are people transitioning to natives, removing non-natives, or removing milkweed completely? Is milkweed abundance changing and how is the species composition of gardens changing?

Objectives and Questions

In Chapter 1, I seek to describe milkweed gardens on a fine scale in a region that has seen increased outside research interest as overwintering western monarch numbers have decreased and reports of winter breeding have increased. As a long-term resident of the community, I also seek to model the importance of place-based science to understanding larger ecological and conservation issues.

My central research question was: What is the prevalence, spatial distribution, and species composition of milkweed gardens of the eastern portion of the San Francisco Bay Area and how are these gardens changing over time? I further divided my central research question into four sub-questions.

(1) How prevalent are milkweed plants in residential gardens in the northern East Bay Area east of the Albany Hill monarch over-wintering site?
(2) What is the species composition of milkweeds in these residential gardens?
(3) How prevalent are native and non-native milkweeds in these residential gardens?
(4) How have the number of milkweed gardens and the species compositions of these gardens changed between 2020 to 2022?

Predictions

I predicted that milkweed gardening would be prevalent, clustered, diverse in species composition, and changing over time. Specifically, I predicted that:

(1) A large number of gardens would include some milkweed species.
(2) Most gardens with milkweeds would include multiple species of milkweeds.
(3) The milkweeds grown would be a mixture of native and non-native milkweeds and that many gardens would include both native and non-native milkweeds.
(4) Milkweed gardens would grow in popularity and that new gardens would cluster near existing gardens through social and ecological dispersal. Given that residents might pass by existing gardens with monarchs during their daily lives, more people would want to enjoy the same monarchs in their own gardens. Additionally, milkweed gardens added over time would reflect the species availability at local nurseries. Native milkweeds would also increase over time. Given the mobility of milkweed seeds and differences in species-specific germination needs, non-native milkweeds would more frequently disperse, germinate, and grow as “volunteers” in new gardens.

METHODS

I began my study during the first summer of the COVID-19 pandemic when travel restrictions by the University of California Berkeley and the State of California made conducting field work and laboratory research difficult. I directed my attention to my own backyard and my surrounding community to formally investigate the patterns in caterpillar diversity and host plant abundance that I had informally observed for many years prior to the pandemic. My formal survey of milkweed began on October 1, 2020, before the historic low winter count of migratory western monarch butterflies in 2020-2021. My survey began before the dates of and without knowledge of another survey of milkweed plants and monarchs in the area (Crone & Schultz 2021). The supplemental analysis included in that survey began on November 29, 2020 and ran through January 11, 2021, only recorded *Asclepias curassavica*, and did not contain the fine scale of resolution nor temporal component of this study (Crone & Schultz 2021). Two other studies focused on the South Bay Area also included information on the greater Bay Area monarch population (James 2024; Schaefer & James 2024). One study included observations of adult monarchs from January 31 to May 31, 2021, and counts of monarch larvae and eggs from February 2 to May 31, 2021. To my knowledge, my study contains the earliest formally recorded observations of this region and population with formal surveys beginning on October 1, 2020, before the start of the 2020-2021 annual overwintering count.

Summary

To understand the prevalence, diversity, and spatial distribution of milkweeds planted by gardeners in an urban matrix, I conducted a survey of a set of neighborhoods delineated by both natural and social features in the eastern portion of the San Francisco Bay Area of California. I surveyed gardens in the fall before significant winter rains when most milkweed vegetation is still green and when dispersing seedpods aid in visually detecting milkweeds from long distances. At this time of year, many plants have flowers and seed pods which aid in identifying species. I surveyed 2256 land parcels representing gardens from October 1 to November 24, 2020. I recorded the presence or absence of milkweed plants in the genus *Asclepias* and in related genera *Gomphocarpus* and *Oxypetalum* in each garden. For gardens with milkweeds, I recorded the species of milkweeds present, the number and size of plants, the general health of plants, and if the plants were located in green strips or front yards. Additionally, I took voucher photos of all plants for comparison over time. I also recorded if monarch larvae were readily visible on plants and recorded detailed counts of monarch larvae and eggs in select gardens. To better understand how milkweed gardens change over time I resurveyed the same gardens from October 14 to November 30 of 2022 following the same protocol and recording the same data recorded in 2020. To determine if the number of gardens growing milkweed changed over the two-year time period, I summed the total number of address points growing milkweed in the surveyed area for each year. To determine if growing native milkweeds changed in popularity, I calculated the percentage of milkweed gardens that included the native milkweeds *Asclepias speciosa* and *Asclepias fascicularis*. In addition to documenting any net changes in the number of milkweed garden numbers and species compositions in the region as a whole, I also followed how individual gardens changed over time.

Study area

Regional landscape

My larger study focused on the residential monarch butterfly population in the East Bay of the San Francisco Bay Area and the milkweed gardens in that region (Figure 1.1). My study focused on two areas within this larger region. The first area was a primarily residential neighborhood east of a monarch overwintering site on Albany Hill. This neighborhood includes portions of the cities of Berkeley, Albany, El Cerrito, and Kensington, California. Elevations range from 14 meters above sea level just above the San Francisco Bay to approximately 150 meters above sea level in the hills below Tilden and Wildcat Canyon Regional Parks. The site includes retail and business properties concentrated along main streets, multiple smaller parks, schools, and a large regional cemetery. Most of the properties are single family homes owned by the residents who occupy those homes. Green strips, strips of public land located between a sidewalk and a road and maintained by adjacent property owners, are present on both sides of most streets but vary in width from city to city. Green strips also vary in the amounts of impervious surfaces such as concrete and in cultivation practices. Lot size and structure placement in lots are relatively uniform in El Cerrito and Albany but differ greatly in higher elevation Berkeley and Kensington. The southwestern portion of this area is also near the University of California Berkeley Gill Tract Farm with another recently documented monarch overwintering population (Xerces 2024). The second area includes the main campus of the University of California Berkeley, the Oxford Tract agricultural field, student gardens, pollinator gardens, and residential lots.

Regional climate

This region has a temperate warm summer Mediterranean climate, Köppen-Geiger climate zone Csb (Beck *et al.* 2018, 2023), characterized by wet, cool winters and warm, dry summers. The highest temperatures of the year are often in September and even into early October. Traditional summer months of June, July, and August are influenced by the coastal fog belt and mornings can be cool and cloudy up until 12 noon or later in the day when the fog layers burn off. Temperatures can vary greatly day to day and nighttime temperatures are lower than daytime, with a difference often greater than in regions with higher humidity. The region has a climate that is very different from many other regions that host monarch butterflies. These unique climatic characteristics influence the growth of milkweed and the times of highest insect activity during the year and during the day. It is common to have days with temperatures over 27 degrees Celsius and even over 32 degrees Celsius well into the end of October. Consequently, plants are still in full growth in the fall. Butterfly activity in the region also peaks in the late summer through the early fall (Shapiro & Manolis 2007).

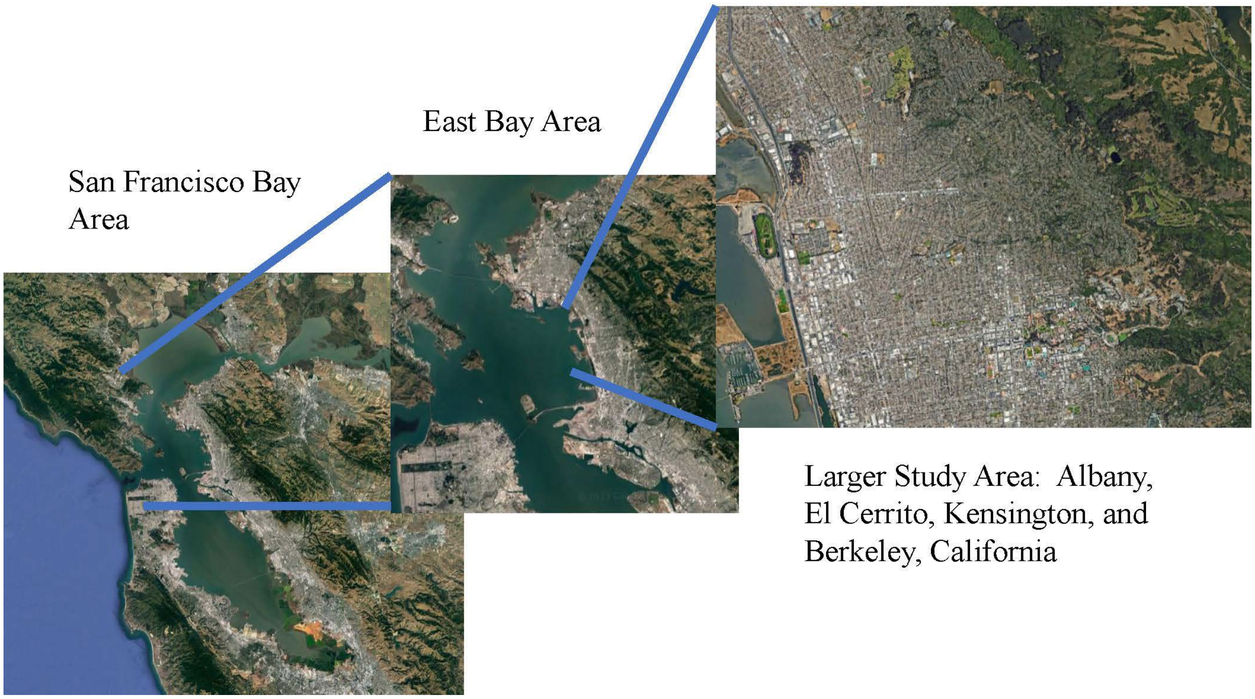

Figure 1.1: Map of study area. A map of the greater San Francisco Bay Area in California showing the larger study area in greater detail (Google Earth 2024).

Vegetation and wildlife

Vegetative cover is high in the area, but landscaping can vary greatly between sections of the site and between adjacent lots within the same section. Lawns are generally uncommon but increase in frequency in portions of El Cerrito and Kensington. Many yards are dominated by drought-tolerant and deer-resistant non-native plants common in the local landscaping industry. Many species are native to South Africa and other regions with a Mediterranean climate. Species of *Salvia* are common as are succulents and euphorbs (Figure 1.2). Residents increasingly choose plants to attract hummingbirds, bees, butterflies, and other wildlife (personal observations). However, the specific species planted are often heavily influenced by the stock of several local nurseries. Native plant gardening has increased in recent years but is still limited (personal observations). Growing food is popular but can be heavily limited by pests and concerns surrounding heavy metal contamination of urban soils (Carpenter & Rosenthal 2011). Wildlife is abundant throughout the site and includes deer, racoons, possums, skunks, foxes, rats, and the occasional coyote (Carpenter & Rosenthal 2011; Peirce 2010; personal observations). Deer populations increase in the hills and their browsing pressure strongly influences gardening practices (personal observations and personal conversations with community members and garden nursery staff).

Figure 1.2: Panel of photos of the common types of gardens in the study area. Lawns are rare, but some gardens, particularly in El Cerrito and the higher elevations of Kensington, contain traditional shrubberies. Some green strips and yards are dominated by weedy plants and others by succulents, cacti, and euphorbs. Pollinator friendly plants including salvias, verbena, and members of the Asteraceae and Lamiaceae are common. Gardens increasingly include natives.

Larger study system: Western monarch butterflies and urban monarchs of the East Bay of the greater San Francisco Bay Area – history, habitat, and current state

Western monarch history in California

Written records of monarchs overwintering in coastal California date back to the late 1800s. The earliest published written record documents monarchs overwintering in Pacific Grove, California in 1874 in an article by the Monterey Weekly Herald (Anonymous 1874; Lane 1993). The earliest scientific records document clusters of overwintering monarchs in 1880 and

1881 (Bush 1881; Lane 1993; Thaxter 1880; Vane-Wright 1993). At the times of these written records, local residents could confirm to the authors that the butterflies gathered for many years prior with an un-named "lady resident" stating that the butterflies had been the same for the twelve years that she had lived in the area (Bush 1881). An early 1914 book on the "butterfly trees" also suggested that these "butterfly trees" had been known to the local residents since the 1860s (Lane 1993; Shepardson 1914). However even earlier written accounts, including those by famed naturalists, make no mention of the winter aggregations (Vane-Wright 1993). There are also not records from earlier Spanish and Mexican colonial periods nor records from local tribes (Lane 1993).

Regular annual counting of overwintering monarch butterflies in California began in 1997 (Malcolm 2018; Xerces Society Western Monarch Count 2024). Fall counting has expanded to include more sites and both Thanksgiving and New Years counting periods. Annual total numbers of butterflies in each count have shown a dramatic decline since 1997 and high variation between years despite the number of surveyed sites increasing (Figure 1.3). Populations typically decrease during January counts after winter storms (Figures 1.4 and 1.5). Some estimates speculate that overwintering butterfly numbers during the 1980s were much higher with at least 4.5 million butterflies (Schultz *et al.* 2017). Based on a quasi-extinction threshold of 30,000 butterflies and maximum likelihood estimates, one study estimates a 50-75% extinction risk within 20 years and a 65-85% extinction risk within 50 years (Schultz *et al.* 2017).

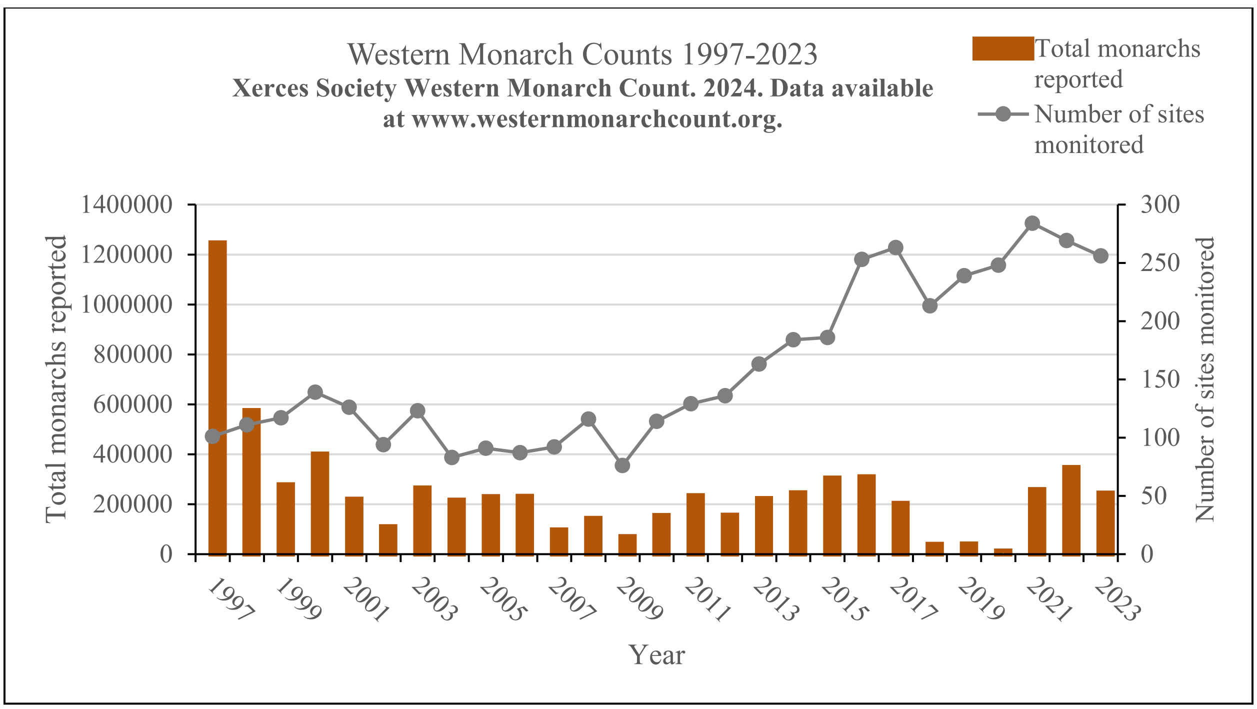

Figure 1.3: Total overwintering western monarch count data and monitoring site data from 1997-2024. The longer running early season counts are often called the Thanksgiving Day Counts. Xerces Society Western Monarch Count. 2024, Current as of March 19, 2024. www.westernmonarchcount.org

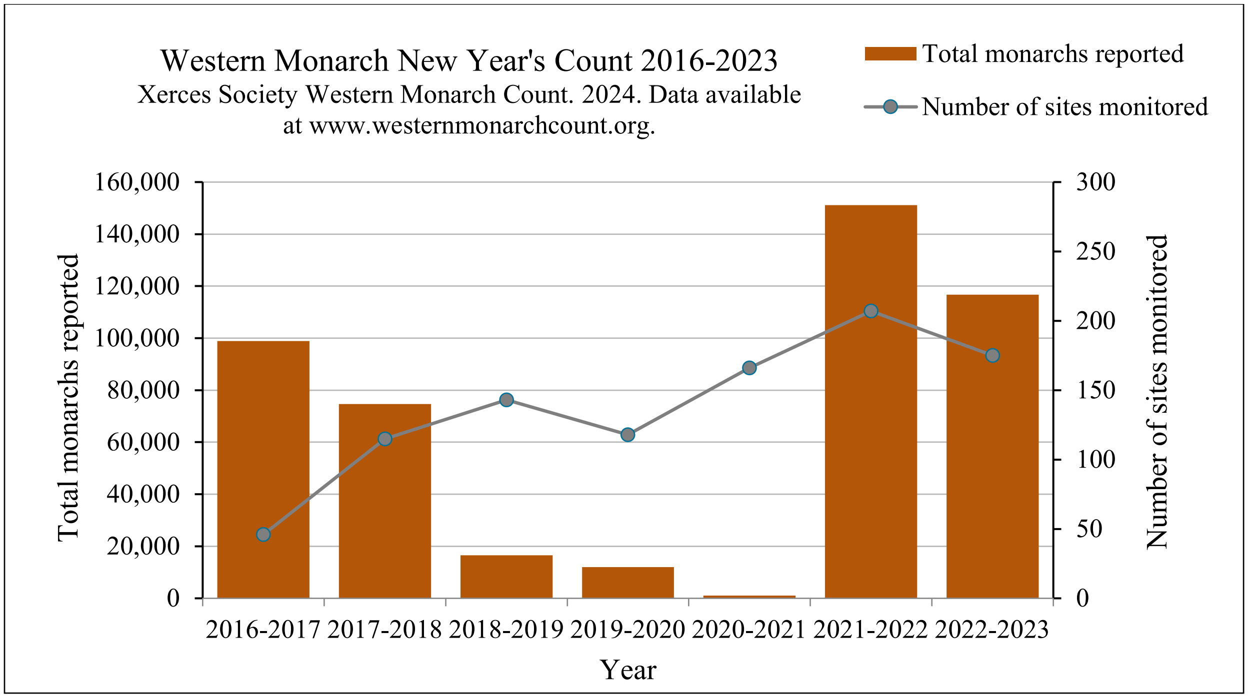

Figure 1.4: Total late season western monarch count from 2016-2024. Xerces Society Western Monarch Count. 2024, Current as of March 19, 2024. www.westernmonarchcount.org

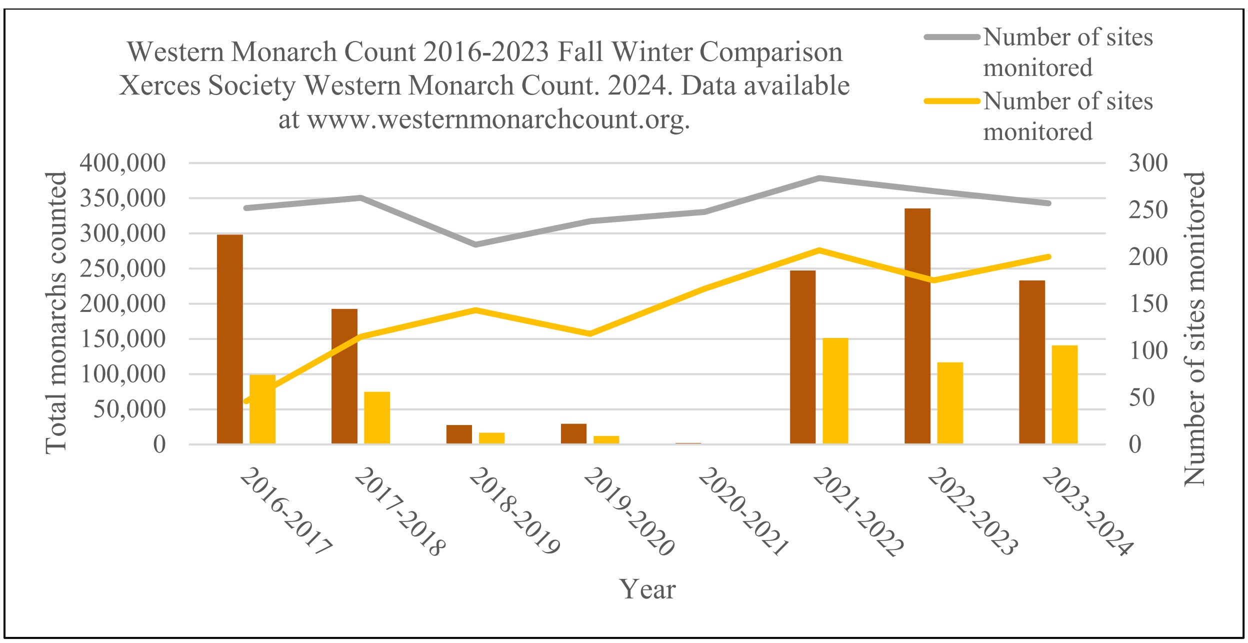

Figure 1.5: Comparisons between early (dark orange) and late (light orange) season counts from when formal late season counts began in the winter of 2016-2017. Lines in gray and light orange represent the number of sites monitored for fall and winter counts respectively. Winter storms typically result in mortality for large numbers of overwintering adult monarchs. Xerces Society Western Monarch Count. 2024, Current as of March 19, 2024. www.westernmonarchcount.org

History of the local monarch butterfly population and near-by overwintering sites

This East Bay Area study region includes at least two monarch overwintering sites. The San Francisco Bay Area monarch population has recently received increased research interest after the record low Thanksgiving count of the 2020-2021 overwintering season (Crone & Schultz 2021; James *et al.* 2021; Schaefer & James 2024).

Albany Hill site

The Albany Hill site is located on the steep slopes of Albany Hill in El Cerrito, California. Overwintering butterflies primarily utilize the non-native blue gum eucalyptus (*Eucalyptus globulus*) trees at the site for roosting. Native live oak (*Quercus agrifolia*) and non-native acacia compose the middle story and the understory is primarily composed of poison oak (*Toxicodendron diversilobum*) (Weiss 2018). Between 1997 and 2023, the site had an overwintering population of between 0 to 3,000 adult monarch butterflies with peaks of over 2,000 in 2011, over 1,200 in 2015, and nearly 600 in 2022. Like other sites, Albany Hill (WMTC site number 2830) has also seen significant variability in counts from year to year with multiple years in the 2000s recording 0 butterflies and only 12 butterflies in 2020 (Xerces Society Western Monarch Count 2024).

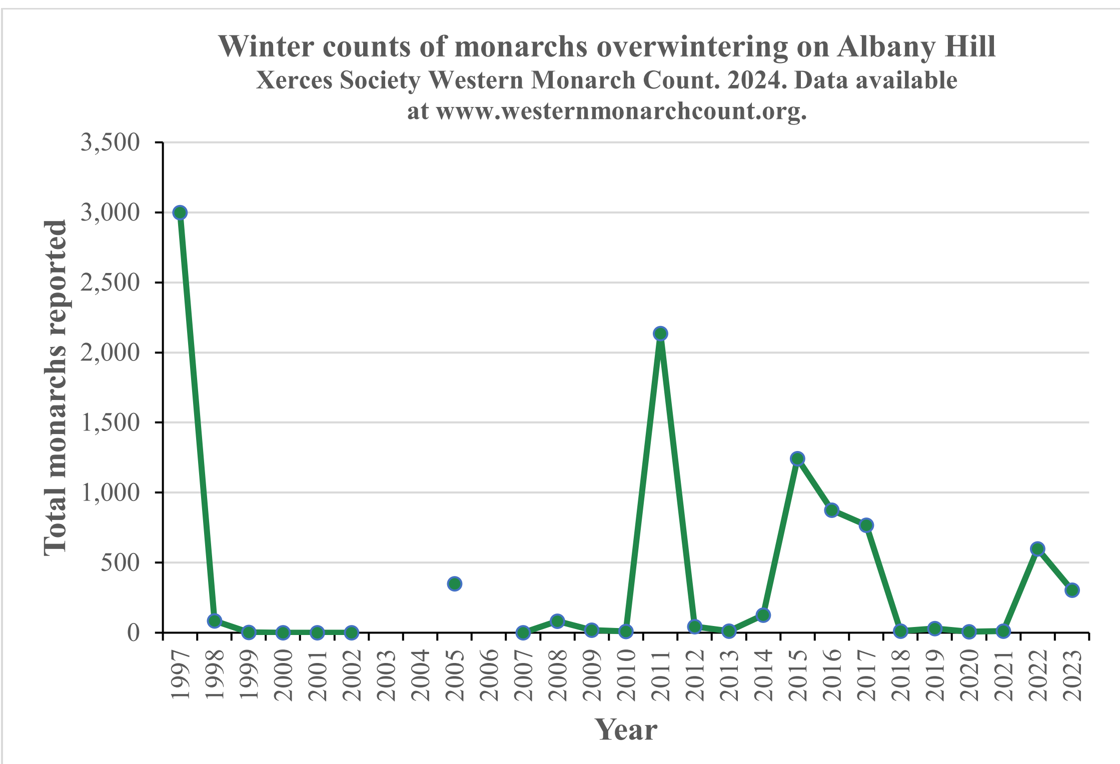

Figure 1.6: Winter counts of overwintering adult monarch butterflies on Albany Hill (WMTC Site 2830) from 1997 to November 2023. Xerces Society Western Monarch Count. 2024, Current as of March 19, 2024. www.westernmonarchcount.org

Gill Tract Community Farm site

A second site is located at the University of California Berkeley Gill Tract Community Farm – originally a plot of over 100 acres purchased by the Gill Family in 1889 and donated to the university for the purposes of agroecological education (Meade & Griffiths 2021). In 1993, the site included a larger coverage of trees with trees existing in the northwestern corner of the plot. These trees decreased by half between June 2007 to August 2009 and, by 2011, most of the trees in this corner of the plot were gone (Meade & Griffiths 2021). Additionally, the University had told community farm staff that they were not allowed to plant new trees in the ground at the site (personal communication with garden staff and ESPM 117 Urban Garden Ecosystems class site visit presentation in 2015). This location had long noted winter aggregations of monarch butterflies utilizing trees at the site, but the site had not been included in the Xerces Society database. An updated 2021 memo to the environmental impact report for development of the site reported that approximately 1,000 monarch butterflies had been seen utilizing the trees in January 1998 (EIP Associates 1997; Meade & Griffiths 2021). During the winter count of 2020-2021, this location was reported to the Xerces Society for inclusion in the annual Thanksgiving counting event (Meade & Griffiths 2021) and the site had a maximum adult monarch butterfly count of 59 in November 2020 (Xerces Society Western Monarch Count 2024). While some butterflies were flying or alone in this total count, a maximum of 27 butterflies were recorded clustering in Monterey cypress (*Cupressus macrocarpa*) and coastal redwood (*Sequoia sempervirens*) on December 2, 2020. The site is now included in annual counting events as Xerces Site 3255 (Xerces Society Western Monarch Count 2024).

Unfortunately, this location continues to face the threat of development for student housing. A portion of the farm was developed into rental properties including retail spaces and a senior living facility by the University of California. This development occurred despite documentation of monarchs overwintering at the site in the draft 1997 (EIP Associates 1997) and in subsequent environmental impact reports. The report noted that “monarch butterflies have been sited [sic] nesting in the eucalyptus stands in the Village and the Gill Tract. The most significant sightings were several years ago on the Gill Tract” (EIP Associates 1997). Furthermore, the report cited phone calls in 1997 with a scientist suggesting that the site was not an aggregation site, but it is not clear if these statements were based on winter surveys (EIP Associates 1997). In 2021, some of the Monterey pine and cypress trees on the site appeared to be dead or dying and some redwoods showed signs of water stress (Meade & Griffiths 2021). Both the Gill Tract site and the Oxford Tract sites have supported adult and larval monarchs and continue to be under threat for development into student housing despite significant mobilization by both undergraduate and graduate students, faculty, and community members (*Occupy the Farm* 2014). Concerns communicated in public comments from both community members and the Xerces Society were acknowledged but largely dismissed in a July 2021 addendum to the original Environmental Impact Report (Rincon Consultants Inc. & University of California, Berkeley Capital Strategies 2021). Several groups have formed a recent partnership to improve the monarch habitat of the Gill Tract with a focus on community events to increase nectar resources for overwintering adult monarch butterflies.

Milkweed garden prevalence and descriptions

Developing a search image

To ensure that my survey would cover all species of *Asclepias* and closely related genera present, I developed a honed search image of species that could theoretically be acquired and planted in regional gardens. To include all species native to or common in California, I consulted the The Jepson Manual for detailed species descriptions (Hickman 1993). Given that most gardeners purchase plants from local sources (personal observation and conversations with gardeners), I reviewed the historic offerings of a popular local plant nursery and made a list of all species of *Asclepias* and related genera offered by that nursery. As a resident of the region from the fall of 2012 through the duration of the study, I was familiar with the offerings of local nurseries and botanical garden sales over the recent years before the survey. I also reviewed the websites of local native plant nurseries. To include species that could have been acquired through the mail, I reviewed *Asclepias* seed distributors listed through the Xerces Society Milkweed Seed finder to include all possibilities that a home gardener could plant. At the time of the survey, many seed distributers were out-of-stock of many species. After developing a species list of plants most offered locally, I reviewed images and morphological descriptions of these and other species to develop a search image (Borders & Mader 2011; Hickman 1993; Motooka 2003; Singhurst *et al.* 2015).

Street surveys: Initial survey in 2020

To determine the prevalence and species composition of urban milkweed plants, I surveyed the green strips and front yards of the study region for all species of milkweed plants present. I conducted my initial mapping and identification of milkweed plants during the fall when milkweed seed dispersal makes plants most visible and when most species have a combination of flowers and seed pods to facilitate identification. I conducted my initial survey from October 1, 2020, to November 24 of 2020 (October 1, 4, 8, 11, November 7, 10, 16, and 24) with over half of the survey occurring between October 1-11 and the majority of the rest occurring by November 10 and a smaller area surveyed on November 16 and 24, 2020. To identify milkweed plants present, I treated public streets as transects and I walked both sides of each street visually scanning the area for all plants in the genera. If an individual plant presented the gestalt of *Asclepias* spp. but did not have flowers, I tested leaves for the presence of latex (if possible) and recorded detailed leaf morphology information and took photos to later confirm uncertain identifications. For some difficult-to-identify plants, I revisited the location multiple times until the plant was flowering to finalize an identification.

After identifying the milkweed species present, I recorded the total number of milkweed plants, the location of the plants within the garden (green space or front yard), the size and general health of the plant, and the street address. I also used a GPS device to record the initial route walked. While I did not formally measure plant size, I took voucher photos of all plants for later review and verification and assigned plants to a size category: seedling, small, medium, large, or clump (when multiple plants covered a large area, and it was impossible or impractical to count the plant number or when multiple stems were likely connected on the same rhizome). When recording plant health, I noted if a plant showed signs of drought stress, a large number of aphids (primarily oleander aphids *Aphis nerii*), large amounts of sooty mold on aphid honeydew, or other specialist milkweed herbivores. While many plants in front yards were too distant to see any monarch larvae or eggs, I recorded if the plant was out of visual range and, when visible, I also recorded if monarch larvae were present on plants and took voucher photos of larvae. To roughly measure monarch larvae usage of plants, I categorized larvae on accessible plants as one of three categories: early instar (first and second instars), mid-instar (third and small fourth instars), or late instar (larger fourth and fifth instars) identifying instars based on a guide by Oberhauser and Kuda (Oberhauser & Kuda, Kristen 1997). All surveys and counts were conducted by the author to ensure consistency of pattern recognition and vision.

Street Surveys: re-survey in 2022

I resurveyed these same transects and parcels from October 14, 2022, to mid-November of 2022 (October 14, October 17; November 3, 4, 6, 7, 11, 13, 16, and 30). I followed the same methods as in 2020 with similar survey effort to ensure that I could locate any new plants.

Percent of gardens with milkweeds in front yards or green strips

To calculate the percentage of gardens surveyed that included milkweeds and to ensure that my survey area was consistent, I recorded each street block surveyed each year and then built a list of all address points surveyed. I downloaded address point data for street blocks surveyed in the cities of Berkeley and Albany from the Alameda County Data Sharing Initiative. When a land parcel contained multiple addresses such as back units and apartment buildings, I counted the parcel as one garden point. I checked the data accuracy against on-the-ground surveys and maps through Google Earth. Given the comparatively smaller number of points and the difficulty in locating address lists for gardens in El Cerrito and Kensington (both in Contra Costa County), I manually entered the address points for parcels visited using Google Map features including maps and satellite view. For a small number of parcels without listed addresses on Google Maps, I used multiple methods to verify address points including Google Street View at different time points to identify address markings on roads and buildings, and on-the-ground verification.

Species composition of milkweed gardens

To describe the species composition of each milkweed garden, I identified each milkweed plant to species and assigned each garden a combined species list for each timepoint visited.

Native and non-native milkweeds

To describe if milkweed gardens were all native, a mixture of native and non-native, or all non-native, I defined native species as milkweed species native to the greater Bay Area. I defined theoretically possible native milkweeds as being in the region at elevations of between 0 to 200 meters above sea level as *Asclepias californica* E. Greene, *Asclepias eriocarpa* Benth., *Asclepias fascicularis* Decne., *Asclepias speciosa* Torrey, and *Asclepias vestita* Hook. & Arn. based on ranges and elevations reported in The Jepsen Manual (Hickman 1993). After surveying, I only encountered *Asclepias fascicularis* and *Asclepias speciosa* and treated only those two species as "native." I defined species native to other regions of California such as *Asclepias linaria* Cav. as being "non-native." I also defined species of *Asclepias* that are native to the United States as being “non-native” and species of *Asclepias*, *Oxypetalum* and *Gomphocarpus* from other global regions as being “non-native” (Endress *et al.* 2014).

Changes in milkweed gardens from 2020 to 2022

To determine if a species of milkweed became more or less common within milkweed gardens, I counted the total number of gardens containing each milkweed species each year and divided that number by the total number of milkweed containing gardens for that year to obtain a percentage of milkweed gardens containing that specific species.

Comparison with other areas

Throughout 2020, 2021, and 2022 I conducted additional walking surveys of new areas. I utilized the same methods as my original surveys. These surveys provided me with additional insight into milkweed gardening in the region and allowed me to compare species compositions in other areas.

RESULTS

Milkweed garden prevalence and description

Milkweed species located

During the surveys, I identified nine species of milkweeds. I located individual plants of six species of *Asclepias*: *Asclepias fascicularis*, *Asclepias speciosa*, *Asclepias curassavica*, *Asclepias tuberosa*, *Asclepias linaria*, and *Asclepias incarnata*. The vast majority of *Asclepias* plants present were *A. speciosa, A. fascicularis*, or *A. curassavica* (Figures 1.7, 1.8, and 1.9). Other species were very uncommon with only two sightings of *A. tuberosa* and one sighting each of both *A. linaria* and *A. incarnata*. I located two species of *Gomphocarpus*: *Gomphocarpus physocarpus* and *Gomphocarpus cancellata* and one species of *Tweedia/Oxypetalum*: *Oxypetalum coeruleum* (Endress *et al.* 2014). While *Gomphocarpus physocarpus* (Figure 1.10) was very common and appeared to frequently disperse to neighboring gardens, I only located two individual plants of *Gomphocarpus cancellata* (Figure 1.11) and one of those plants died during the study period (personal conversation with gardener). The species that I located were consistent with the plant species that had been available at local nurseries and botanical gardens.

Street surveys: Initial survey in 2020

During the initial survey period of October 1 to November 24, 2020, I surveyed 2256 address points for milkweeds in green strips and front yard gardens. These parcels represented a walking distance of approximately 36.5 km. Of these 2256 points, 90 gardens contained milkweeds in the front yards or green strips that were visible from the sidewalk. If the gardens in which I did not locate milkweeds represent true absences, most gardens did not contain milkweed in 2020.

Plants in most front yards were too far away to effectively count larvae or eggs. Out of these 90 gardens in the core sampling area, I was able to locate one or more monarch larvae in 38 of the gardens. I took more detailed larvae counts in 33 of these 38 gardens (Table 1.1). Monarchs continued to oviposit on both native and non-native milkweeds well into November of 2020 often with high densities of eggs (Table 1.1; Figures 1.12, 1.13, 1.14, 1.15).

Figure 1.7: Examples of *Asclepias speciosa* located on October 1, 2020, in Berkeley, California.

Figure 1.8: *Asclepias fascicularis* in Berkeley and and El Cerrito, California. Left to right, taken on October 1, October 11, and November 10, 2020. Plants showed considerable phenotypic variation with less irrigation and higher sunlight leading to very narrow leaves and more irrigation and shade leading to wider leaves with deeper greens. I also noted variation in the amount of pink pigment in flowers which can be the result of growing conditions.

Figure 1.9: *Asclepias curassavica* in Berkeley, California. Taken on October 1, 2020.

Figure 1.10: *Gomphocarpus physocarpus* in Berkeley and El Cerrito, California. Left to right, photos taken on October 8, November 6, and November 7, 2020.

Figure 1.11: *Gomphocarpus cancellata* growing in Berkeley, California. From left to right, the first two photos on October 1, 2020, show growth habit and latex presence and the third photo taken on January 9, 2021, shows details of floral morphology.

Street Surveys: re-survey in 2022

During the re-survey period of October to November of 2022 (October 14, 17; November 3, 4, 6, 7, 11, 13, 16, and 30), I again surveyed 2256 address points for milkweeds in green strips and front yard gardens. Of these points, 127 number of gardens contained milkweeds in the front yards or green strips that were visible from the sidewalk in 2022 (Table 1.2). If the gardens in which I did not locate milkweeds represent true absences, most gardens did not contain milkweed, but the number that did increased.

Table 1.2: Parcels surveyed, gardens containing milkweed, and breakdowns of gardens containing all native, a mixture of native and non-native, and all non-native milkweeds for the fall of 2020 and the fall of 2022.

Years surveyed	2020	2022
Total points surveyed	2256	2256
Number of core surveyed gardens with milkweeds	90	127
Number and percent of gardens with:		
- Native milkweeds only:	12 (13.3%)	18 (14.2%)
- Native and non-native milkweeds:	8 (8.9%)	17 (13.4%)
- Non-native milkweeds only:	70 (77.8%)	92 (72.4%)

Table 1.1: Monarch larvae and egg counts in a subset of gardens. Abbreviations represent the first letters of species and genus names.

Date of observation	Garden	Species in Garden	Species with Larvae	Total Larvae Count	EI count	MI count	LI count	Egg count
10/1/2020		AC AS	AC	2	1	1		
10/1/2020		AC	AC	13		7	6	
10/1/2020		AC	AC	2			2	
10/1/2020		AC	AC	1			1	
10/1/2020		AC	AC	1			1	
10/4/2020		AC AF	AC	3		2	1	
10/4/2020		AC	AC	1		1		
10/4/2020		AC AS	AC	6		3	5	
Total gardens: 8				Total larvae: 29				
10/8/2020		AC	AC	4	2	2		
10/11/2020		AC	AC	7	2	4	1	
10/11/2020		AF AS	AF AS	5	2	1	2	
10/11/2020		AC AS	AC	3	1	1	1	
10/11/2020		AC	AC	5	5			
10/11/2020		AC	AC	1	1	1		
Total gardens: 6				Total larvae: 25				
11/6/2020		AC	AC	2		2		
11/6/2020		AC	AC	5		5		
11/6/2020		AC GP	GP	4			4	
11/7/2020		AC	AC	13	1	6	6	
11/7/2020		AC GP AS	GP	4	1	2	1	
11/7/2020		GP	GP	1	0	1	0	
11/7/2020		AS	AS	11	6	5		19
11/7/2020		GP	GP	18			18	
11/7/2020		AC	AC	3	3	0	0	12
11/7/2020		AC	AC	16	0	12	4	
11/7/2020		AC	AC	1	0	1	0	
11/7/2020		AC	AC	4		1	3	
11/7/2020		GP	GP	12	5	6	1	
Total gardens: 13				Total larvae: 94				Total eggs: 31
11/10/2020		AS	AS	6	6	0	0	49
11/10/2020		AC	AC	4	4	0	0	27
11/10/2020		AC	AC	1			1	
11/10/2020		AC	AC	3	3	0	0	
11/10/2020		AF	AF	7	2	5	0	
11/10/2020		AC	AC	20	3	3	14	
Total gardens: 6				Total larvae: 41				Total eggs: 76

Figure 1.12: New growth of native milkweed *Asclepias speciosa* on November 10, 2020, with high densities of monarch larvae and eggs. I counted 26 small stems of new growth of *Asclepias speciosa* with a total of 6 small larvae and 49 eggs on these stems on November 10, 2020. This garden had previously had all of the green strip and parts of the front yard dominated by *A. speciosa* in the early summer and the plants had been removed around the time of the parcel changing ownership. This new growth may be the result of resprouting rhizomes after high fall temperatures.

Figure 1.13: Monarch larvae and eggs on native *Asclepias speciosa* in a green strip in El Cerrito, California on November 7, 2020. Three stems of *A. speciosa* in a green strip had 11 monarch larvae and 19 eggs despite two of the plants being largely defoliated and the other being trampled.

Figure 1.14: Monarch larvae on native *Asclepias fascicularis* on November 10, 2020, in Berkeley, California.

Figure 1.14: Monarch larvae on *Asclepias curassavica* in Berkeley and El Cerrito, California. Photos taken on November 7 and 11, 2020.

Figure 1.15: Monarch larvae and eggs on non-native *Gomphocarpus physocarpus* in El Cerrito, California. Photos taken on November 7, 2020.

Changes in milkweed gardens from 2020 to 2022

Milkweed gardening expanded over the two-year period with a higher number of gardens growing milkweed in the same area in 2022 versus 2020. Only four species of milkweeds were regularly found in gardens: *Asclepias fascicularis, Asclepias speciosa, Asclepias curassavica, and Gomphocarpus physocarpus*. More gardens contained native milkweeds in 2022, with the percentage of milkweed-containing gardens natives *Asclepias fascicularis* and *Asclepias speciosa* both increasing by 4.5 percentage points over the two years, from 8.9% in 2020 to 13.4% in 2022 for *Asclepias fascicularis* and from 14.4% in 2020 to 18.9% in 2022 for *Asclepias speciosa*. Many gardens still contained non-native milkweeds in 2022. The percentage of milkweed growing gardens with non-native *Asclepias curassavica* decreased by 4.8 percentage points from 73.3% in 2020 to 68.5% in 2022, but the percentage growing non-native *Gomphocarpus physocarpus* increased by 7.3 percentage points from 10% in 2020 to 17.3% in 2022 (Table 1.3).

Table 1.3: Number and percentages of milkweed gardens containing each species by year. Percentages represent the percentage of milkweed gardens that include each species for both 2020 and 2022. Change between years reflects the absolute change in percentages from 2020 to 2022 values.

	2020	2022	Change between Years (percentage points pp)
Total points surveyed	2256	2256	
Number of core surveyed gardens with milkweeds	90	127	
Number of and percent of milkweed growing gardens containing each species of milkweed:			
- *Asclepias fascicularis* Decne.	8 (8.9%)	17 (13.4%)	+ 4.5 pp
- *Asclepias speciosa* Torrey	13 (14.4%)	24 (18.9%)	+ 4.5 pp
- *Asclepias curassavica* L.	66 (73.3%)	87 (68.5%)	-4.8 pp
- *Gomphocarpus physocarpus*	9 (10%)	22 (17.3%)	+ 7.3 pp
- *Gomphocarpus cancellata*	2 (2.2%)	1 (0.8%)	-1.4 pp
- *Asclepias linaria* Cav.	0 (0%)	1 (0.8%)	-0.3 pp
- *Asclepias incarnata*	0 (0%)	1(0.8%)	+ 0.8 pp
- *Oxypetalum coeruleum*	1 (1.1%)	4 (3.1%)	+ 2.0 pp
- *Asclepias tuberosa*	1 (1.1%)	2 (1.6%)	+ 0.5 pp

DISCUSSION

Discussion introduction

In Chapter 1, I sought to describe milkweed gardens on a fine scale in a region that has seen increased research interest as overwintering western monarch numbers have decreased (Crone & Schultz 2021; James *et al.* 2021; Schaefer & James 2024). As a long-term resident of the community, I also sought to model the importance of place-based science to understanding larger ecological and conservation issues. My central research question was: What is the prevalence, spatial distribution, and species composition of milkweed gardens of the eastern portion of the San Francisco Bay Area and how are these gardens changing over time? I further divided my central research question into four sub-questions.

Milkweed prevalence in residential gardens of the East Bay

My first sub-question was: (1) How prevalent are milkweed plants in residential gardens in the northern East Bay Area east of the Albany Hill monarch over-wintering site? I found that while milkweed was common in gardens, these gardens only represented a small percentage of land parcels. I had predicted that a large number of gardens would include some milkweed species. There is great potential to expand the number of gardens containing milkweeds and other plants providing larval food resources and nectar for butterflies and other pollinators.

Species composition of milkweed gardens

My second sub-question was (2) What is the species composition of milkweeds in these residential gardens? I found that there was a mixture of native and non-native milkweeds in gardens and that only a small number of species were found in gardens. I predicted that most gardens with milkweeds would include multiple species of milkweeds.

Native and non-native milkweeds

My third sub-question was (3) How prevalent are native and non-native milkweeds in these residential gardens? Many gardens contained both native and non-native milkweeds, but there were many gardens with only native or only non-native milkweeds as well. A large number of gardens only contained *Asclepias curassavica*. I had predicted that the milkweeds grown would be a mixture of native and non-native milkweeds and that many gardens would include both native and non-native milkweeds.

Changes in milkweed gardens from 2020 to 2022

My fourth sub-question was (4) How have the number of milkweed gardens and the species compositions of these gardens changed between 2020 to 2022? I found that milkweed gardens increased in number over the two-year period. For the same area, there were 127 gardens containing milkweed in 2022 compared to 90 in the same area at the same time of year in 2020. This result aligned with my prediction that milkweed gardens would grow in popularity and that, after re-surveying the same area, I would record more gardens with milkweed in 2022 than in 2020.

I predicted that while milkweed gardens added over time would reflect the species availability at local nurseries, native milkweeds *A. fascicularis* and *A. speciosa* would become more common in gardens. I also predicted that milkweeds native to the larger region in California including *Asclepias californica*, *Asclepias eriocarpa*, and *Asclepias vestita* would start to be encountered in gardens. I also expected to encounter *Asclepias cordifolia*. Native milkweeds *A. fascicularis* and *A. speciosa* did become more common in gardens containing milkweed, but not to the degree that I had anticipated. Additionally, I did not encounter other species of milkweed that I thought might begin to appear in gardens. I encountered one plant of *Asclepias cordifolia* in a campus pollinator garden outside of the core study area and that plant was not thriving.

There could be numerous factors impacting this pattern. Native milkweeds *A. fascicularis* and *A. speciosa* continued to be difficult to obtain through 2021 (personal observations). As I worked to grow my supply of both species, nursery staff at one trusted local nursery informed me that the plants sold as soon as they came in (personal communication with staff). Additionally, lines for entry into nurseries were long when social distancing was enforced, and gardening appeared to dramatically increase in popularity. During and after the spring of 2022, I noted that *A. fascicularis* became more easily obtainable in local nurseries. In one garden, I noted new *A. speciosa* plants and small *A. fascicularis* plants in a green strip between the survey periods but only the *A. speciosa* survived to be counted in 2022. While I did not re-survey gardens in the fall of 2024, anecdotally, I do have the sense that native milkweeds are continuing to become more prevalent.

Obtaining plants that had not been exposed to pesticides was also difficult, potentially influencing plant choice. After obtaining native milkweed plants from a different un-named nursery, I observed that larvae feeding on the new plants died shortly thereafter. Other gardeners reported to a colleague that their larvae also died after feeding on new plants (personal communication with Patina Mendez). These observations of pesticide prevalence are consistent with studies published around the same time period demonstrating the ubiquity of pesticides in milkweeds and the difficulty in tracking the exposure of plants to pesticides in nurseries (Halsch *et al.* 2020, 2022). Additionally, a large regional nursery began notifying customers that they were required to treat their plants with *Bt* and advising gardeners to net their plants for their first year (observed in nursery catalog, signage, and personal communication with staff). It is possible that gardeners could not predictably access native milkweeds or gave up.

In my own attempts to grow other *Asclepias* species from the western United States from seed, I could successfully germinate plants, but they failed to thrive in commercial potting mixtures. While the health of these plants improved after I amended soil for higher drainage and decreased water availability, time constraints made daily care by me impractical, and they did not survive overwatering by undergraduate staff. These specialized needs of species like *Asclepias cordifolia* are well documented and others have found that they grow poorly in peat-based media with both seedlings and rhizomes quickly succumbing to root rot (Landis & Dumroese 2015). In my own garden native milkweeds also frequently died of root rot during the wet Bay Area winters when planted in a variety of potting soils marketed as being high end and environmentally friendly (personal observations). To maximize the chance of success, gardeners wanting to grow native milkweeds in pots should mix their own potting soil mixtures specific to individual species needs utilizing the resources cited in this chapter (Borders & Lee-Mäder 2014; Landis & Dumroese 2015).

Given the mobility of milkweed seeds and differences in species-specific germination needs, I predicted that non-native milkweeds would more frequently disperse, germinate, and grow as "volunteers" in new gardens. Many plants of *A. curassavica* appeared to have been volunteers from neighboring gardens, but most plants appeared to have been planted or purposefully cared for after dispersing. While visiting plants, especially while counting monarch larvae, some gardeners introduced themselves to me and were excited to learn about my research and to tell me about their own gardens. Several were able to tell me about the origins of their plants. One gardener with large stands of *A. speciosa*, informed me that the plants were volunteers that had dispersed from an adjacent lot behind the garden on another street. The parent plants were in a garden of predominantly native plants. Given that many native milkweeds require special treatment and time to establish from seeds, I expected volunteer native plants to be rare. Plants of *A. speciosa* in this garden consistently remained healthy throughout each season and regularly supported monarch larvae (personal observations 2020-2024). After obtaining permission, I collected seeds from these plants and germinated them in July of 2022 without cold-moist stratification and only by pre-soaking in water and received high germination rates. Given the wide variation in germination needs of seeds from different populations of the same *Asclepias* species, it is possible that the parent plant was from a population that more readily germinated (Kaye et. al 2018, Landis and Dumroese 2015, Bandara et. al 2019). At least one gardener informed me that their *Gomphocarpus physocarpus* plant was a volunteer that they kept after enjoying monarch larvae.

Given that residents might pass by existing gardens with monarchs during their daily lives, I predicted that more people would want to enjoy the same monarchs in their own gardens and would want to plant milkweed as a result. Originally, I had hoped to complete a final chapter in this manuscript to survey and interview gardeners and began drafts of that survey, but I later determined that such a chapter would be complicated by how recent regulations surrounding monarchs in California might impact an IRB approval. It is my recommendation that future regulations should allow more flexibility and support to a diverse range of researchers, especially to researchers with smaller citizen science and NGO groups, early career researchers, and researchers operating with fewer funding and laboratory resources. Supporting a broad range of scientists from different backgrounds and institutions is important to representing the views of local communities impacted by science. Additionally, while I did predict that new gardens would cluster spatially and I did record locations, a full spatial analysis is not included in this study due to privacy concerns and time and resource constraints.

Early fine scale data on monarchs and milkweeds in an area of conservation concern

To my knowledge, my study contains the earliest formally recorded observations of this region and population. My formal survey of milkweed began on October 1, 2020, before the historic low winter count of migratory western monarch butterflies in 2020-2021. My survey began before the dates of and without knowledge of another survey of milkweed plants and monarchs in the area (Crone & Schultz 2021). The supplemental analysis included in that survey began on November 29, 2020 and ran through January 11, 2021, only recorded *Asclepias* *curassavica* and did not contain the fine scale of resolution nor temporal component of this study (Crone & Schultz 2021). My study initially surveyed the majority of gardens during the first eleven days of October (23 gardens on October 1, 2020; 5 gardens on October 4, 2020; 14 gardens on October 8, 2020; 12 gardens on October 11, 2020) and the remainder during the first portion of November 2020 (20 gardens on November 7, 2020; 9 gardens on November 10, 2020; 5 gardens on November 16, 2020; and 2 gardens on November 24, 2020). Native milkweeds were still green during this time period, and I was able to record all milkweeds present. As a long-term member of the community, I was also able to revisit some gardens throughout the year. Knowledge of the extent of milkweeds in urban areas in general is still surprisingly scarce and recent, making any knowledge of urban systems important (Johnston *et al.* 2019).

Limitations and future directions

Limitations

My study is limited in that it only includes milkweeds grown in front yards and green strips, likely leading to an underestimate in milkweed gardening. However, I do believe that the publicly visible front yards and green strips in the area are good representations of milkweeds grown. The placement of structures in area lots leads to a large amount of total garden space being visible. Norms in this area include little to no lawns and the presence of deer browsing and lack of front yard fences may lead to people planting deer-resistant low maintenance plants in front yards and green strips. Milkweeds are generally ignored by deer and well-established milkweed plants, especially natives grown in the ground, are resistant to drought requiring little to no irrigation. These factors make milkweeds ideal for front yards and green strips. I expect that protected back yards are more likely to have plants for consumption and plants needing deer protection. Additionally, I have noted that gardeners growing milkweeds tend to have the plants throughout their yards. Some gardeners have indicated that they plant milkweed so that the public can enjoy the larvae (personal communication with gardeners and publicly visible signage in some gardens). This is in line with the norms of neighborhoods in this region. Foot traffic is common and residents, especially in Berkeley, practice forms of public giving making front yards more of a quasi-public space than is common in many residential areas. Little Libraries are common and "free piles" – boxes or displays of goods for donation to passersby are ubiquitous. Planting milkweeds and pollinator gardens in spaces viewable to the public such as bike trails and schools has also been suggested as a way to support monarchs while also promoting environmental education (Landis 2014). I consistently found milkweed plants in locations such as schools, church gardens, and garden sections of parks. I expect that front yard and green strip surveys might underestimate some rare milkweeds which people might have protected in fenced yards, but my extensive growing experience and the documented difficulty in growing many species leads me to believe that these rare species are very rare indeed in gardens (Borders & Lee-Mäder 2014; Landis & Dumroese 2015).

Another potential limitation for my study is my potential impact on gardening activities. I completed online Human Research Subjects Social Sciences Training and exercised due caution in my work. I quickly realized that garden owners and the general public were extremely enthusiastic to communicate with me about milkweed. On one occasion in the fall of 2020, an unknown man stopped his vehicle in the middle of a road to yell with excitement "*Asclepias*, right?!" On a different occasion in the same time period a postal worker asked me "What are you doing with that *Asclepias*?" On yet another occasion, two cyclists passed by me one saying to the other "I need to plant way more milkweed this year." To not influence gardener behavior, I would often conduct surveys during the workday to minimize my interactions and impact. If people were present in a garden or adjacent gardens, I revisited the location on another day to minimize my impact. When gardeners asked me for advice, I referred general questions to the Xerces Society website. If asked I did not tell gardeners which species of milkweeds to plant, but instead advised that they keep their plants pesticide free and healthy and refocused on encouraging them to practice observing their own gardens as an ecological system and recording their observations. If questioned about removing non-natives, I advised gardeners that part of the purpose of my study was to have scientifically backed locally relevant advice and that I did not want to advise removing something without a nuanced understanding of the system. Given my precautions and the comparatively small percentage of gardeners who approached me relative to the number of gardens, I believe that I did not significantly impact milkweed gardens. Additionally, gardeners who approached me had very well cared for gardens that stayed similar throughout the two years and were informed that I was a researcher. I cannot eliminate the possibility that scientists from other groups or agencies may have interacted with gardeners. One study did conduct monarch counts after my initial 2020 survey in part of this study region from November 29 to January 11 as part of a population estimate, but details of the locations were not published and I did not have knowledge of the survey (Crone & Schultz 2021). I encountered a researcher affiliated with the group tagging adult monarch butterflies near my home around the border of the study area during my daily commute in the summer of 2022. I do not know to what extent other scientists may have interacted with gardeners and could not control for this impact.

Another potential limitation is the fact that my surveys were conducted in October and November and there is a chance that some individual native milkweed plants may have already died back. However, I believe that this is unlikely as both *Asclepias fascicularis* and *Asclepias speciosa* both retain green vegetation and actively support monarch larvae well into November and often farther into the winter (Table 1.1, Figures 1.12, 1.13, 1.14; Chapter 2 of this manuscript). Some individual plants will partially die back in parts of the summer, but such plants will generally resprout new growth in early fall and will remain visible. Old, desiccated stems of *Asclepias speciosa* and their seed pods are often not cut back (personal observations) and I was consistently able to identify these species at long distances. If I did miss plants of *Asclepias fascicularis* and *Asclepias speciosa*, this would have been slightly more likely in 2022 as more of the re-survey dates were in the later parts of October and November, which would have made the increase in natives only larger, not altering the general pattern of both natives increasing in their relative prevalence in milkweed gardens. Additionally, the climate was similar in both years.

There is a small possibility that I might not have recognized some species of milkweed, but I find this highly unlikely. I was able to identify a specimen of *Asclepias linaria* based on vegetation alone without having previously viewed this species in person. I conducted all of the surveys personally and devoted a consistent survey effort per distance in both the initial survey and resurvey. Given the long distances walked, I took brakes approximately every two hours and frequently re-checked the first and last blocks of a survey period to ensure that accuracy did not decrease due to fatigue.

While my initial survey area choice had some bias due to pandemic shelter in place restrictions, I believe that the breakdown in milkweed species is representative of Berkeley, El Cerrito, Kensington, and northern Oakland, California. While not included in the data presented in this chapter, I surveyed additional regions using the same methods presented here from 2020 to 2022. I expanded this initial area to the west farther toward Albany Hill in the late winter of 2021 and to the south in adjacent neighborhoods with standard lot sizes and shapes. I also surveyed an additional stretch to the east farther into the hills above the core study area in 2020 but did not fully resurvey this area in 2022 due to the high variation in lot size and shape; the frequent lack of sidewalks and green strips; and the fact that many lots in the hills facing the west had structures placed closer to roads making garden visibility inconsistent. I also surveyed a smaller region north and west of the University of California Berkeley campus, and two areas to the southeast of the Gill Tract. I also opportunistically surveyed other stretches as walking transects through Berkeley. For some of these small regions I had some blocks missing in either 2020 or 2022 and excluded them for consistency. While it is more difficult to follow those locations through time, the milkweed gardens that I did record had similar species compositions.

Future directions

Extrapolating milkweed prevalence and diversity data more generally to the greater Bay Area should include randomly generated points and routes and should ensure that extrapolations consider lot size, structure type, community norms, structure ownership, property values, and amounts of impervious surfaces and lawns. Blocks with apartments often had higher amounts of impervious surfaces and it is more difficult for residents to have any control over landscaping when they are not owners. If surveys hope to infer conservation intent represented by gardens, it is important to consider if residents have any autonomy over gardens. Urban data on milkweed density is still relatively scarce, but the importance is increasingly being recognized and more researchers are considering how urban areas can increase milkweed abundance (Johnston *et al.* 2019). Future studies should include the social study of gardener motivations and practices that I had planned but did not have the time or resources to implement. Ideally, such a study should be done by someone in the local community who understands the practices and motivations of people who rear monarchs. After changes in regulations and conservation messaging, obtaining accurate information in interviews will require that gardeners can trust and feel heard by researchers. Public social media and online forums already indicate distrust of some regulations and conservation messaging with members of the public indicating that they will be "bootlegging butterflies" a reference to rearing and protecting larvae regardless of rearing prohibition. I recommend that agencies allow private citizens to rear small numbers of monarch larvae for the educational benefits and ecological connections that they provide. Best practices can also be better communicated to the public when the public trusts agencies.

Additionally, locations that support monarchs in a way that allows community members to enjoy butterflies in the urban environment should not be destroyed to build new structures. It is my recommendation that the plans to build student housing and real estate properties at the Gill Tract farm be cancelled. This land should be allowed to continue to support research and education in environmental science, agroecology, and agriculture as these uses best support the intended purpose of the land and are aligned with protecting monarchs.

Broader implications

Given the changing nature of our world, conservation practitioners should approach monarchs and milkweeds as the complex system that they are and share this complexity with the public. The vast majority of conservation discourse focuses on the adult butterfly stage of monarchs and its migratory and overwintering patterns. Much less attention is given to monarch larvae and the complexities of their interactions with their host plants, especially outside of laboratory settings. Not all milkweed is equal. There can be large variations both between and within species of milkweeds. Changes in environmental conditions can change how a milkweed plant impacts a monarch larva.

Conservation groups should carefully craft conservation outreach and messaging and should evaluate if the public has the resources to carry out the recommendations. Outreach should specify if a particular conservation recommendation is based on data from the local region, the larger western monarch population, or extrapolated to a population based on studies of monarchs in the eastern United States. Recommendations should include more complex information about the diversity of milkweeds and the evolutionary ecology of their relationship with monarchs. Most importantly, statements indicating delineated rules should include citations of publications that are not behind a paywall and that are available in full to members of the general public.

Implicit in the discourse surrounding Bay Area monarchs is the idea that there is a right kind of monarch and a wrong kind of monarch. If urban monarchs are viewed as a threat to migration, people in urbanized areas are forced to consider forgoing their milkweed gardens and their enjoyment of butterflies so that they can be enjoyed inland and to the north by other communities. Not everyone has the resources to be able to travel to larger parks and protected areas. While surveying a garden of *A. curassavica* in a commercial part of Berkeley, a woman passed me saying “I love how they’ve created a little butterfly sanctuary.” Moments later a man said, “he misses the butterflies from Alabama,” as he pushed an elderly man in a wheelchair past the nectaring monarchs. The perceptions of urban nature can have an uncomfortable history reflecting racial and class dynamics. It is important for conservation decision makers to remember that science is for everyone and so are the butterflies.

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Chapter 2: Winter maintenance practices of residential milkweed gardens and the availability and use of winter milkweed vegetation by monarch butterflies in the northeastern San Francisco Bay Area

ABSTRACT

North American monarch butterflies (*Danaus plexippus* (L.)) migrate each fall to either the mountains of central Mexico or the coasts of California. Scientists have long noted that some monarchs continue to breed during the winter months and may reside in a given location year-round. Winter breeding of monarchs in California has become a growing concern as annual overwintering adult numbers have decreased. While climate change is clearly part of the cause of the winter breeding pattern, conservation rhetoric has focused on the role of non-native milkweeds. I documented the winter availability of milkweeds in the eastern portion of the San Francisco Bay Area during the winter of 2020-2021. I re-visited gardens identified during the fall of 2020 and followed how milkweed plants were maintained throughout the winter. After recording if non-native milkweeds were cut back during the winter, I classified the degree of pruning and recorded the presence or absence of monarch larvae. Additionally, I conducted more detailed counts of larvae and eggs on select plants. For gardens containing non-native milkweeds, I found that approximately 18% of such gardens are well pruned close to the ground leaving little to no vegetation, an additional 15% have plants that are partially pruned, and approximately 67% appear to not be pruned at all. Monarch adults, larvae, and eggs are present in local gardens throughout the duration of the winter but are less common in late January through mid-February. Many larvae present in the first two weeks of January 2021 were fourth and fifth instar larvae remaining from the previous year. Large concentrations of eggs became common in early March of 2021 with high egg densities on many plants. While non-native milkweeds were available to and used by monarchs during winter months, some native *Asclepias fascicularis* and *Asclepias speciosa* plants retained green vegetation into mid-January of 2021, calling into question the assumption that all native milkweeds die back during the winter. Some plants of *Asclepias fascicularis* from different sources maintained green vegetation throughout the duration of winter months, potentially benefiting from warmer microclimates associated with structures and underground systems. Plants subsequently grown in a greenhouse from seed from two such plants remained green throughout winter months when grown without artificial lighting in a room above outside temperatures, suggesting that a naturally decreasing photo period was not cueing dormancy. All plants of *Asclepias speciosa* grown in the same greenhouse room died back in the winter, suggesting that the plants were cued by decreasing day lengths. From 2020 through 2024, I encountered plants of both species of milkweeds remaining green into the fall including to the north and at high elevations in the eastern Sierra Nevada. Conservation practitioners should consider the future impact of rising temperatures on the growth of all species of milkweed. They should also consider that many factors beyond if a plant is native are likely impacting monarchs during the winter.

INTRODUCTION

Milkweed plants in residential gardens have become increasingly common, but surprisingly little formal documentation of milkweeds in urban systems exists (Johnston *et al.* 2019). The mismatch between conservation pushes to plant milkweed and the nursery industry's ability to meet resulting consumer demand has resulted in an urban habitat matrix of largely non-native milkweeds. While monarchs can utilize non-native milkweeds and many gardeners report that monarchs prefer the non-natives (personal conversations with gardeners), conservation groups and scientists have also expressed concern over how non-native milkweeds can impact monarchs. Arguments against non-native milkweeds have historically tended to focus on one species, *Asclepias curassavica*, and how that species can influence monarch migratory behavior, chemistry, and disease prevalence.

Conservation groups argue that non-native milkweeds disrupt natural migratory cycles by encouraging monarchs to breed when they would otherwise be overwintering (Majewska & Altizer 2019; Steele *et al.* 2023). Winter breeding by monarchs in the United States was first documented in the 1960s in populations in Arizona, outside of San Diego, California, and in Florida (Brower 1961; Funk 1968; Urquhart *et al.* 1970). However, this winter breeding behavior has long existed in other regions throughout the Pacific and in other countries that monarchs have colonized (Hemstrom *et al.* 2022; Malcolm 2018; Vane-Wright 1993; Zalucki & Clarke 2004). While not all monarchs migrate, migration is the standard pattern for monarchs in North America. It has now been accepted that monarchs breed during the winter months throughout much of the southeastern United States and that the monarchs in southern Florida form a year-round resident population (Brower 1961; Knight & Brower 2009; Steele *et al.* 2023). Documentation of and concern about winter breeding monarchs in California has continued to grow. Populations have been documented in the Los Angeles and San Francisco Bay areas, however very little information has been formally gathered about these locations (Crone & Schultz 2021; James *et al.* 2021; Schaefer & James 2024).

Monarchs are not restricted to one species of milkweed and successive generations are exposed to multiple species as they move across the landscape, all with different characteristics. These milkweed species can vary greatly in qualities that impact growing larvae and adult butterflies, from specific cardenolide chemical profiles, overall levels of cardenolides, amounts of latex, and other factors (Agrawal *et al.* 2015). Many environmental variables can impact these qualities of milkweed (Decker *et al.* 2018; Decker & Hunter 2020; Faldyn *et al.* 2018). Such variation exists not only between but also within individual species of milkweed. Additionally, changes in environmental variables can impact the properties of one species of milkweed, but not another (Faldyn *et al.* 2018). Variation in the chemistry of milkweeds can also impact larval resistance to disease (Decker *et al.* 2018; Majewska & Altizer 2019).

Perhaps the greatest concern leveled toward non-native milkweeds is that they concentrate the prevalence of larval infection by a specialist protozoan *Ophryocystis elektroscirrha* (*OE*) in populations of monarchs (Satterfield *et al.* 2015, 2016). In the eastern United States, winter-breeding monarchs have a much higher proportion of butterflies that are heavily infected with *OE* (Satterfield *et al.* 2015). Another study found that adult monarchs sampled in gardens with winter breeding showed an infection risk that was nine times higher than in adult monarchs sampled in overwintering aggregations in coastal California (Satterfield *et al.* 2016). *OE* can harm monarchs in many ways, reducing longevity, flight performance, and mating success and also reducing body size and leading to deformities in wings (Altizer & De Roode 2015). A compromise has been to encourage gardeners to cut back their non-native milkweeds during the winter. However, it is not clear if people follow the recommendations.

Objectives and Questions

My central research question for chapter 2 was: How do residential gardening practices influence the availability of milkweed vegetation during the winter months and how extensively is this vegetation used by winter breeding monarch butterflies? I further divided this question to four sub-questions:

1. How abundant is milkweed vegetation in urban gardens during the winter months and which species of milkweeds are most prevalent during the winter months?
2. How are non-native milkweeds with active winter foliage maintained by gardeners? Do gardeners cut back milkweed plants during the winter and, if so, how much do they prune the plants?
3. How prevalent is year-round breeding on non-native milkweeds that are not cut back during the winter?
4. Do native milkweeds truly die back during the winter months?

Predictions

I predicted that:

1. Milkweed vegetation would be common throughout the winter and that the majority of these plants would be *Asclepias curassavica.*
2. Milkweed vegetation management would vary greatly from garden to garden and that gardens would either contain plants that were all well-pruned closely to the ground removing the majority of leaves or not pruned at all with plants remaining similar sizes and shapes throughout the seasons and retaining leaves throughout the winter.
3. Monarch eggs, larvae, and adults would remain common throughout the winter and that adults would continue to oviposit on new growth.
4. Native milkweeds would die back fully during the winter months.

METHODS

Study area

Regional landscape

My larger study focused on the residential monarch butterfly population in the East Bay of the San Francisco Bay Area and the milkweed gardens in that region (Figure 2.1). My study focused on two areas within this larger region. The first area was a primarily residential neighborhood east of a monarch overwintering site on Albany Hill. This neighborhood includes portions of the cities of Berkeley, Albany, El Cerrito, and Kensington, California. Elevations range from 14 meters above sea level just above the San Francisco Bay to approximately 150 meters above sea level in the hills below Tilden and Wildcat Canyon Regional Parks. The site includes retail and business properties concentrated along main streets, multiple smaller parks, schools, and a large regional cemetery. Most of the properties are single family homes owned by the residents who occupy those homes. Green strips, strips of public land located between a sidewalk and a road and maintained by adjacent property owners, are present on both sides of most streets but vary in width from city to city. Green strips also vary in the amounts of impervious surfaces such as concrete and in cultivation practices. Lot size and structure placement in lots are relatively uniform in El Cerrito and Albany but differ greatly in higher elevation Berkeley and Kensington. The southwestern portion of this area is also near the University of California Berkeley Gill Tract Farm with another recently documented monarch overwintering population (Xerces 2024). The second area includes the main campus of the University of California Berkeley, the Oxford Tract agricultural field, student gardens, pollinator gardens, and residential lots.

Regional climate

This region has a temperate warm summer Mediterranean climate, Köppen-Geiger climate zone Csb (Beck *et al.* 2018, 2023), characterized by wet, cool winters and warm, dry summers. The highest temperatures of the year are often in September and even into early October. Traditional summer months of June, July, and August are influenced by the coastal fog belt and mornings can be cool and cloudy up until 12 noon or later in the day when the fog layers burn off. Temperatures can vary greatly day to day and nighttime temperatures are lower than daytime. There can also be considerable fine scale micro-climate differences which impact growing conditions (Carpenter & Rosenthal 2011; Peirce 2010). The region has a climate that is very different from many other regions that host monarch butterflies. These unique climatic characteristics influence the growth of milkweed and the times of highest insect activity during the year and during the day. It is common to have days with temperatures over 27 degrees Celsius and even over 32 degrees Celsius well into the end of October. Consequently, plants are still in full growth in the fall. Butterfly activity in the region also peaks in the late summer through the early fall (Shapiro & Manolis 2007).

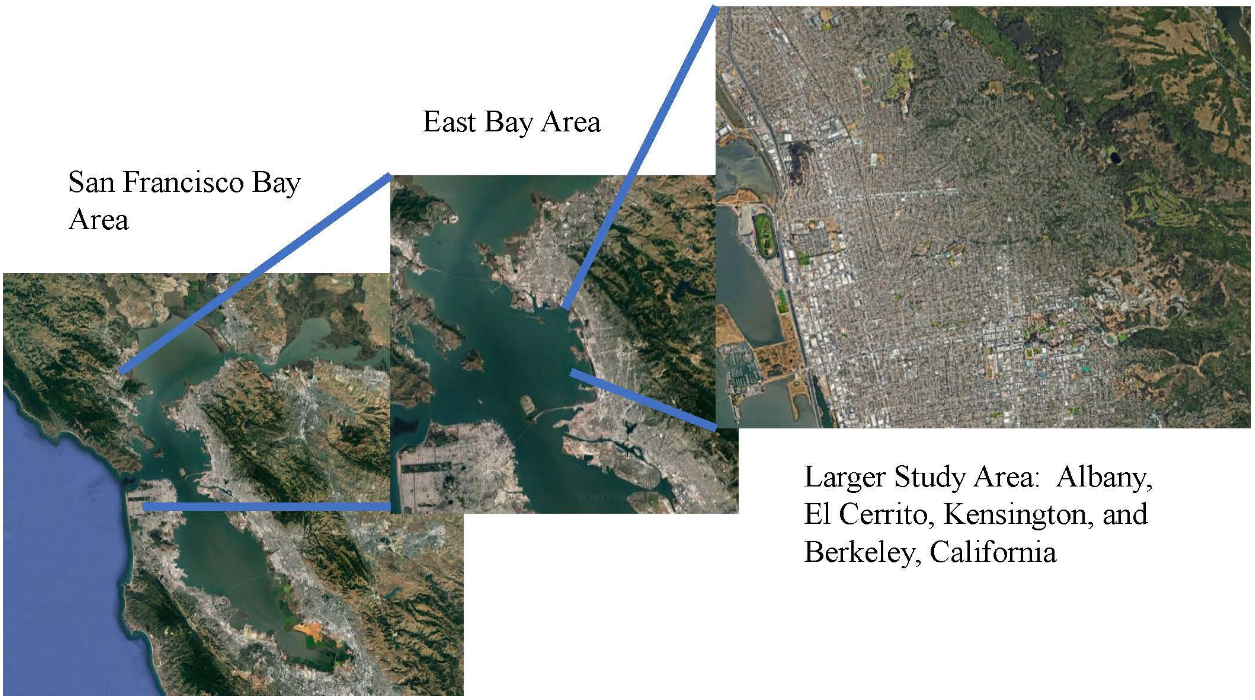

Figure 2.1: Map of study area. A map of the greater San Francisco Bay Area in California showing the larger study area in greater detail (Google Earth 2024).

Larger study system: Northeastern San Francisco Bay urban monarchs and milkweed gardens

History and conservation of Western monarch population and near-by overwintering sites

While discourse surrounding monarch butterflies has historically focused on the eastern population which overwinters in Mexico, written records of monarchs overwintering in costal California date back to the late 1800s (Anonymous 1874; Bush 1881; Lane 1993; Thaxter 1880; Vane-Wright 1993). Regular annual counting of overwintering monarch butterflies in California began in 1997 (Malcolm 2018; Xerces Society Western Monarch Count 2024). These annual counts have shown a dramatic decline since 1997 and high variation between years (Xerces Society Western Monarch Count 2024). Some estimates speculate that counts during the 1980s were much higher with at least 4.5 million butterflies overwintering annually in coastal California (Schultz *et al.* 2017). The monarch population faces many threats (Crone & Schultz 2021; Jepsen & Black 2015; Malcolm 2018; Pelton *et al.* 2019; Schultz *et al.* 2017) which I also detail in Chapters 1 and 3 of this manuscript. Two overwintering sites are located in this larger study area (Xerces Society Western Monarch Count 2024). Research and conservation interest in the Bay Area population of monarchs has increased after the record low winter count of overwintering western monarchs (Crone & Schultz 2021; James *et al.* 2021; Schaefer & James 2024).

Distribution, species composition, abundance, and winter availability of milkweed species

Residential cultivation of milkweed is common and is growing in popularity, however very few species are commonly grown in this area. Only four species of milkweeds are regularly encountered in local residential gardens: *Asclepias curassavica*, *Asclepias fascicularis*, *Asclepias speciosa*, and *Gomphocarpus physocarpus*. Species rarely encountered include: *Gomphocarpus cancellata*, *Asclepias incarnata*, *Asclepias tuberosa, Asclepias linaria*, and *Oxypetalum coeruleum* (Chapter 1 of this manuscript).

Winter availability of milkweed vegetation

Revisiting gardens from October and November 2020

To determine winter availability of milkweed, I revisited milkweed gardens identified during my initial surveys in the fall of 2020. I included all of the gardens that I had identified in October and November of 2020 including those that I excluded from my 2020 to 2022 comparison for various reasons detailed in Chapter 1. I revisited gardens from December 27, 2020, to March 13, 2021, with the majority of visits occurring between January 8 to February 23, 2021. Visit dates were December 27, 2020; January 8, 9, 10, 13, 14, 17, and 19; February 9, 23, and 27; and March 1, 2, 5, 11, and 13 of 2021.

This time period is after the start of cold temperatures and winter rains and during the time when native milkweeds are thought to be dormant and when adult monarchs are thought to be clustered in overwintering locations. All March visits were to gardens that I had previously visited in January or February and these visits were intended to observe the transition between winter and spring monarch patterns which can vary each spring depending on weather. I visited previously identified gardens, grouped by location, and recorded milkweed vegetation that could be oviposited on by adult monarchs and subsequently consumed by larval monarchs.

Additional gardens surveyed

I also surveyed new locations throughout the winter of 2021. From February 12 to 21, I surveyed a new region expanding the western border of my core study area closer to Albany Hill. I surveyed the new region on February 12, 18, and 21, 2021 utilizing the same methods as Chapter 1 while also recording details of milkweed maintenance. While I did not initially anticipate being able to locate native milkweeds, I was often able to identify larger plants of *Asclepias speciosa* by remnants of seed pods and dead stems. On some occasions, such gardens would have large numbers of native plants.

I combined the re-surveyed gardens with the new additional gardens surveyed to determine the amount and species composition of milkweeds that are available to monarchs during the winter.

Winter maintenance of milkweed plants

Resurvey of gardens from the fall of 2020

While conducting the winter visits described above, I recorded detailed information about the maintenance states of the milkweed plants that I located. Conservation messaging to the public often cites October as the time at which gardeners should cut back their non-native milkweeds. However, both native and non-native milkweeds in the study area remain green with active monarch larvae well into November. As winter storms result in tree debris and more non-milkweed species of plants dying back in the coldest days of the year, gardeners might begin pruning milkweed as part of general storm clean-ups and preparations for spring gardening (personal observations). Based on this logic, I determined that re-visiting gardens in the end of December through the early part of January would be most likely to reflect purposeful pruning of milkweed. I expected that gardeners who would intentionally prune milkweed would do so by that time. I revisited the majority of gardens for the first winter visit between December 27, 2020, to January 19, 2021, with the majority of visits occurring on January 9 and 14, 2021. While visiting each garden, I checked plants for signs of pruning and took voucher photos of each milkweed plant present. When possible, I also visited gardens for a second winter visit to document any additional trimming performed later in the winter. I conducted these additional visits between February 21 to March 13, 2021, with the majority occurring in February of 2021.

Classification of milkweed maintenance

To group general patterns in milkweed winter maintenance, I initially assigned each garden to one of 3 groups – cut back, partially cut back, and not cut back. I classified gardens as cut back if they had all milkweed plants cut back close to the ground with a consistency that suggests they did so purposefully to follow guidelines shared in science media. At the end of the season, some gardeners will cut back the majority of their milkweed plants and move remaining larvae to one or two plants that they leave uncut to feed the larvae until they pupate (personal observation and conversations with gardeners). I grouped these gardens with those classified as cut back. If gardens had only some of the milkweed plants cut back or if plants only indicated light pruning that might be done to all plants in the winter, I classified this as partially cut. If gardens had milkweed that remained intact with little or no maintenance through the winter, I classified these gardens as not cut back (Table 2.1).

While in the field, I assigned each garden a category, made additional notes about the pruning, and took voucher photos. To ensure that my categorization was consistent, I later viewed the winter voucher photos and visually compared them to the initial survey photos in the fall of 2020. As I visited gardens, I noted that some native milkweeds were not dying back and retained green or yellow-green foliage during the winter and other native milkweed plants retained the brown dead stems from the previous season. I classified these plants as: native not cut brown or native not cut green. If a garden contained only native milkweeds and those had completely died back or had been cut back making no part of the plant visible, I classified these plants as native not visible (Table 2.1).

Table 2.1: Criteria for classification of milkweed maintenance categories.

Maintenance Category	**Criteria for Category**
Cut back	Plants show clear evidence of intentional pruning with plants pruned to sizes much smaller than during the fall, mostly lacking leaves, often pruned within 6-12 inches from the ground, and pruned more heavily than other plants in the same garden.
Partial	Plants may be pruned back slightly but still retain leaves and/or some plants may meet the cut back criteria, but many plants do not meet the cut back criteria.
Not cut	Plants show no evidence of intentional pruning and plants remain a similar size and shape from fall to winter.
Native not cut brown	Plants must be *Asclepias fascicularis*, *Asclepias speciosa*, or another *Asclepias* native to the larger region as defined in Chapter 1. Plants do not have active growth but still retain old, dried stems from the previous season which have not been intentionally cut back
Native not cut green	Plants must be *Asclepias fascicularis*, *Asclepias speciosa*, or another *Asclepias* native to the larger region as defined in Chapter 1. Plants have active growth that could be consumed by monarch larvae and these plants have not been cut back. Plants may have a mixture of dead and green stems.
Native not visible	Plants must be *Asclepias fascicularis*, *Asclepias speciosa*, or another *Asclepias* native to the larger region as defined in Chapter 1. Plants must not be visible despite being documented in the previous fall.

Figure 2.2: Examples of plants in the “cut back” category. Photos on the left taken on October 1, 2020, show the plant healthy and in full growth. Photos to the right show the same plants photographed on January 10, 2021. Both plants are well-pruned and close to the ground. A third plant on the top right is pruned in the same manner. Only a small amount of vegetation on a fourth plant retains leaves, likely left to support the remaining larvae.

Figure 2.3: Examples of plants in the “cut back” category with a remaining plant stem and larvae. A green strip containing *Asclepias curassavica* in Berkeley, California photographed left to right on October 1, 2020, and January 9, 2021. Details show that the plants have been cut back close to the ground. Many pruned plants still contain a small number of leaves. Pictured is one plant with remnants of foliage and two large monarch larvae feeding on the plant. Gardeners who cut back milkweeds frequently leave select plants to support the larvae that remain in their gardens.

Figure 2.4: An example of a cluster of milkweed plants that meet the not cut back category. The top photo shows plants on October 1, 2020, and the bottom photo shows the same plants on February 9, 2020.

Winter use of milkweeds by monarch butterflies

While it was often not possible to determine if larvae or eggs were present on plants in front yards, I recorded if it was possible to see the presence or absence of larvae from the street or sidewalk and, if it was possible, I recorded the presence or absence of larvae as: larvae present or larvae absent for plants that I could physically inspect or none readily visible for plants that did not appear to have larvae from a visual inspection. When it was possible to physically inspect the plant for detailed larvae and egg counts, I identified larvae according to a published field guide (Oberhauser & Kuda, Kristen 1997), counted eggs, and took voucher photos. I grouped larvae into 3 size classes as described in Chapter 1: early instar (first and second instars), mid-instar (third and smaller fourth instars), and late instar (larger fourth and fifth instars). I also recorded any pupae that I encountered; however, larvae generally do not pupate on the host plant, and I did not actively search for pupae on other plants to minimize my time in each garden and respect privacy. Although a number of gardeners had given me permission to enter front yards and sometimes back yards to count larvae and larval predators for Chapter 3, I found that this drew attention from residents and passersby and made data quality less consistent because I might spend 30 minutes to an hour discussing biocontrol of aphids and gardening practices for attracting natural enemies of garden pests instead of counting eggs. Thus, I restricted my counts to plants in green strips or that were within physical reach of sidewalks and roads.

Late fall and winter dormancy of native milkweeds

To determine if native milkweeds die back during the winter, I opportunistically monitored plants of *Asclepias fascicularis* and *Asclepias speciosa* from November 2020 to December of 2024 for evidence of greenery and growth during late fall and winter. When I encountered a plant of *Asclepias fascicularis* and *Asclepias speciosa* with green growth in late fall through winter, I recorded the location of the plant, the date of the observation, took a dated voucher photo of the plant, and automatically uploaded the photo to online storage for a digital timestamp. When access and permission allowed, I also archived seeds from the plant. Additionally, I periodically monitored winter growth and dormancy of each species in my population of greenhouse grown plants. These plants did not receive supplemental light, received a natural photo period, and were grown at temperatures slightly above outdoor winter temperatures (approximately 18 degrees Celsius lows at night and 24 degrees Celsius highs for day).

RESULTS

Winter availability of milkweed vegetation

I was able to re-visit 110 gardens identified during the fall of 2020 on at least one date in the winter of 2021. I completed these first winter visits between December 27, 2020, through February of 2021. I also located an additional 12 gardens containing milkweed in a new survey area closer to Albany Hill during surveys on February 12, 18, and 20. While some plants are intentionally pruned (described below) and others die back fully or partially (described below), there is still an abundant supply of milkweed during the winter months. While the majority of this milkweed was *Asclepias curassavica*, *Gomphocarpus physocarpus* was common and a small amount of foliage on native milkweeds *Asclepias fascicularis* and *Asclepias speciosa* was also present. Additionally, I found that vegetation of *Gomphocarpus cancellata*, *Asclepias linaria*, and *Oxypetalum coeruleum* was available during the winter.

Winter maintenance of milkweed plants

Classification of milkweed maintenance

Most gardens either met the criteria for cut back or not cut back. Given that many gardens contained multiple species of milkweeds, I assigned the garden one maintenance category for the whole garden. If a garden had native milkweeds that were not cut back but also non-native milkweeds that were not cut back, I classified the garden as not cut and not one of the native categories. Only gardens that only contained natives were assigned to one of the native categories. I classified gardens as other if I could not locate a non-native milkweed plant, likely indicating that the plant had been removed or had died between fall and the winter points.

Gardens with fall 2020 and winter 2021 comparisons

I was able to re-visit 53 of these gardens two or more times during the winter through early spring of 2021. I completed the majority of the first visits to evaluate winter milkweed and monarch activity from January 8 to January 14, 2021, with one occurring earlier on December 27, 2020. I completed the majority of second visits on February 23 and 27, 2021; with a small number of second visits on February 9 and 17 visits in early March (March 2 to 13). While I was not able to visit them two times, I was able to visit another 57 gardens from the fall of 2020 one time each from January 8 to March 13, 2021, with the majority – 46 out of 57 – of gardens visited between January 8 to February 23, 2021. In total, I visited 53 gardens at at least three time points (1 during fall and 2 during winter) and an additional 57 gardens at two time points (1 during fall and 1 during winter) for a total of 110 gardens with fall to winter comparisons.

The vast majority of the 53 gardens that I visited two or more times during the winter did not change pruning states between the first early and second late sample dates. Only 7 out of 53 gardens had a state change, with only 2 changing from not cut to cut, 4 changing from not cut to partial, and 1 changing from partial to cut back. Of the 4 gardens that changed from not cut to partial, 1 was a single tweedia (*Oxypetalum coeruleum*) plant that was cut back and the other was a garden that did not intentionally prune milkweed (personal conversation with gardener, location and photos not included to protect gardener privacy). Although monarch larvae can feed on *Oxypetalum coeruleum*, adult monarchs rarely oviposit on the plants even when *O. coeruleum* plants are near other milkweeds (personal observations, unpublished data of regular egg counts in garden of author). Given that the first winter visit consistently documented winter pruning in the cut back category, I combined all 110 gardens (Table 2.2).

Table 2.2: Number and percentage of gardens in each milkweed maintenance category

	Maintenance Category					
	Cut Back	Not Cut	Partial	Native	Other	Total Gardens
Number of gardens with 1 visit:	9	32	7	4	1	53
Number of gardens with 2 visits:	8	30	7	6	6	57
Total number of gardens:	17	62	14	10	7	110
Percentage of gardens in each category:	15.5%	56.4%	12.7%	9.1%	6.4%	
Number of non-native gardens:	17	62	14			93
Percentage of gardens in each category:	18.3%	66.7%	15.1%			

Additional gardens surveyed during the winter and early spring of 2021

I located an additional 12 gardens containing milkweed in the new survey area closer to Albany Hill during surveys on February 12, 18, and 20. All but 2 of these 12 only contained *Asclepias curassavica*, with 1 containing *Gomphocarpus physocarpus* and another containing the dried remnants of an *Asclepias speciosa* plant. Only 2 of the 12 met the criteria for the cut back category, 1 for the partial, and 1 for native not cut back. The percentages of each maintenance category were similar to that of the other sample (Table 2.2) despite a small sample size: 16.7%, 66.7%, 8.3%, and 8.3% respectively for cut back, not cut, partial, and native not cut. Because I had not previously sampled these locations, I could not determine if the area contained gardens meeting the native not visible maintenance category.

Winter use of milkweeds by monarch butterflies

Monarch larvae and eggs on winter foliage

Monarch larvae were present in gardens every month of my observations from October 1, 2020, through March of 2021. Many plants located in front yards were too far away to see larvae. For plants that were accessible, many did not have larvae during the winter. Larvae were more common during the first three weeks of January as larvae from earlier in the winter approached pupation. It was often not possible to conduct detailed counts of eggs and larvae. The species of milkweeds in area gardens during the winter often have complex branching and narrow leaves making it challenging to accurately count larger plants. Whenever possible, I completed more detailed counts of larvae and eggs for select accessible gardens (Tables 2.3, 2.4, 2.5).

Table 2.3: Presence or absence of monarch larvae in gardens aggregated by day and month. The table presents the number of gardens visited on each date; the number of gardens that have larvae present, do not have larvae present, or cannot be assessed due to distance by date; and the aggregated counts for each category by month.

Dates of observations	**Gardens visited**	**Gardens with larvae present**	**Gardens without larvae present**	**Gardens out of view**
December 2020				
12/27/2020	2	2	0	0
Monthly totals:	2	2	0	0
January 2021				
1/8/2021	8	1	3	4
1/9/2021	3	2	1	0
1/10/2021	6	2	3	1
1/13/2021	13	4	9	0
1/14/2021	28	5	19	4
1/17/2021	9	3	6	0
1/19/2021	7	0	4	3
Monthly totals:	74	17	45	12
February 2021				
2/9/2021	7	1	5	1
2/12/2021	6	0	5	1
2/18/2021	5	0	3	2
2/20/2021	2	0	2	0
2/23/2021	18	0	16	2
2/27/2021	10	1	6	3
Monthly totals:	48	2	37	9
March 2021				
3/1/2021	2	2	0	0
3/2/2021	6	1	3	2
3/5/2021	5	1	3	1
3/10/2021	2	1	1	0
3/11/2021	7	3	2	2
3/12/2021	8	0	7	1
3/13/2021	5	0	5	0
3/16/2021	1	0	1	0
3/17/2021	7	0	3	4
3/19/2021	2	0	2	0
Monthly totals:	45	8	26	10

Table 2.4: Counts of monarch larvae and eggs for select gardens in January and February 2021. Abbreviations indicate the first letter of plant genus and species names. Total larvae include all three groups (EI (first and second instars), MI (third and small fourth instars), and LI (large fourth and fifth instars). Detailed egg counts were only done in February. Counts with a plus indicate that the count was an approximation and counts are the stated number or larger. The two counts with an asterisk represent that the breakdown of larval categories was not collected for that point, but that the majority were LI.

Date	**Milkweed species with larvae or eggs**	**Total larvae**	**EI count**	**MI count**	**LI count**	**Egg count**	**Pupae count**
January							
1/9/2021	AC	2+			2+		
1/10/2021	AC	1		1			
1/10/2021	AC	1+			1+		
1/14/2021	GP	5			5		
1/14/2021	AC	1			1		
1/14/2021	AC	1			1		
1/14/2021	AC	1			1		
1/14/2021	GP	50+*					
1/17/2021	AC	1			1		
1/17/2021	GP	7*					
February							
2/9/2021	AC	0				15	
2/9/2021	AC	1			1	---	
2/9/2021	AC	0				5	
2/9/2021	AC	0				20	
2/12/2021	AS	0				0	1
2/23/2021	GP	0				15	
2/23/2021	GP	0				4	
2/27/2021	GP	0				7	3
2/27/2021	GP	3		2	1	13	
2/27/2021	AC	0				2	

Table 2.5: Counts of monarch larvae and eggs for select gardens in March 2021. Abbreviations indicate the first letter of plant genus and species names. Total larvae include all three groups (EI (first and second instars), MI (third and small fourth instars), and LI (large fourth and fifth instars). Dashes indicate that data was not collected for that item.

Date	Milkweed species with larvae or eggs	Total larvae	EI count	MI count	LI count	Egg count	Pupae count
March							
3/1/2021	AC	3	3			---	
3/1/2021	AC	1	1			10	
3/2/2021	AC	1	1			12	
3/2/2021	AC	0				16	
3/2/2021	AC	0				2	
3/5/2021	AC	1		1		6	
3/5/2021	AC	0				1	
3/5/2021	AC	0				8	
3/10/2021	AF	0				77	
3/10/2021	AC	2	2			6	
3/11/2021	AC	6	6			64	
3/11/2021	AC	1	1			1	
3/11/2021	AC	2	2			25	
3/12/2021	AC	0				5	
3/12/2021	AC	0				7	
3/12/2021	AC	0				2	
3/13/2021	AC	0				16	
3/13/2021	AC & GP	0				12	
3/17/2021	AC	0				6	
3/17/2021	AC	0				0	
3/19/2021	AF	0				113	

Some gardens contained large numbers of larvae during mid-January, most of which were fourth and fifth instars. One plant of *Gomphocarpus physocarpus* had over 50 larvae on January 14, 2021 (Figure 2.5). This plant also had pupae on adjacent fencing (Figure 2.5). I also noted that both larvae and pupae were present on a large plant of *Gomphocarpus cancellata* (Figure 2.6). This South African species of milkweed was rare in the area having, to the best of my knowledge, only been sold by one local nursery in 2016 (2016 catalogue, nursery name excluded for privacy).

Figure 2.5: High densities of monarch larvae on a *Gomphocarpus physocarpus* plant in El Cerrito, California on January 14, 2021. Red circles on the top image and bottom close-up images show monarch larvae. Yellow circles show pupae. The density was so large that it was difficult to count every larva and I stopped counting at 50.

Figure 2.6: Photos of *Gomphocarpus cancellata* growing in Berkeley, California on January 9, 2021. The bottom row of photos also taken on January 9, 2021, show multiple monarch larvae feeding on the same plant as well as a pupa on the plant.

Urban egg loading

Egg density was often high on plants that I visited during the early spring of 2021. During March of 2021, I observed an extremely dense patch of monarch eggs on a small patch of emerging *Asclepias fascicularis* adjacent to the Oxford Tract facility on the campus of the University of California Berkeley. In this small area, I counted 77 monarch eggs on March 10, 2021 (Figures 2.7 and 2.8). On March 19, 2021, I counted 113 monarch eggs in the same location all in the same patch of *Asclepias fascicularis*. This was the most extreme case of urban egg loading that I witnessed, but generally high densities of monarch eggs on small plants are extremely common in this region (personal observations from 2020 to 2024 including unpublished regular egg counts of plants in the garden of the author and in select campus gardens).

Figure 2.7: High densities of eggs on early spring growth of *Asclepias fascicularis* in Berkeley, CA. Photos taken on March 10, 2021, show a small area of new growth with 77 eggs and closer images of 2 areas of stems in the patch.

Figure 2.8: Close up of high densities of eggs on early spring growth of *Asclepias fascicularis* in Berkeley, CA. Photos taken on March 10, 2021.

Late fall and winter dormancy of native milkweeds

Asclepias fascicularis and Asclepias speciosa in the Bay Area

Many native milkweed plants retained green vegetation well into the late fall and early winter for both *Asclepias fascicularis* and *Asclepias speciosa* (Chapter 1 and Figures 2.9 and 2.10). Additionally, some plants of *Asclepias fascicularis* remained green throughout the entire winter (Figure 2.11) during some years. These plants were in different locations and from different sources including two plants that I could trace to two different nurseries. I could not determine the source of plants in a garden and field on the University of California Berkeley campus but suspect that these plants may have been planted by past staff or dispersed from a former pollinator garden that was being managed by an indigenous students gardening group at the time. While most will die back by January each year, it is not uncommon to encounter monarch larvae feeding on the plants in December (Figure 2.12).

Figure 2.9: *Asclepias fascicularis* remains green well into the winter of 2021 in Berkeley, California. Photo taken on January 13, 2021.

Figure 2.10: *Asclepias speciosa* remains green well into the winter of 2021 in Berkeley, California. Photo taken on January 14, 2021.

Figure 2.11: *Asclepias fascicularis* in protected areas remaining green during winter. The left top and bottom photos show the same plants on December 27, 2022, and January 27, 2023. The photo to the right shows a plant on December 21, 2022.

Figure 2.12: Monarch larvae feeding on two species of native milkweeds in the winter in Berkeley, CA. Many plants of *Asclepias fascicularis* and *Asclepias speciosa* continue to remain green and to support monarch larvae on December 5, 2023.

Asclepias fascicularis and Asclepias speciosa grown in greenhouse conditions

Among greenhouse grown populations of *A. speciosa* and *A. fascicularis*, most plants of *A. speciosa* died back during the winter months and resprouted in the spring. The vast majority of plants of *A. fascicularis* in the same greenhouse rooms remained green with active growth throughout the winter. Although I did not count the plants, I regularly took photos of these plants.

Additional observations of Asclepias fascicularis and Asclepias speciosa in Northern California

I observed specimens of *Asclepias fascicularis and Asclepias speciosa* that remained green during the middle to end of October in higher elevation locations to the north and northeast. I visited the Willits Bypass Mitigation Project lands near Willits in Mendocino County, California after staff had contacted a colleague about predation by invasive mantids on monarch larvae (personal communication with and documentation of mantis predation by Marisela De Santa Anna). I observed plants of both *Asclepias fascicularis and Asclepias speciosa* in October that remained green and with larvae.

During additional travel in the eastern Sierra Nevada in Mono and Inyo counties, I also documented plants of both *Asclepias fascicularis and Asclepias specios*a with green vegetation on October 20, 2023. Some of these plants were at relatively high altitudes (Twin Lakes, California at 7000 ft (2134 m); below Monitor Pass at approximately 8000 ft (2438 m); and near Walker, California at approximately 5400 ft (1646 m)) (Figure 2.13). Additionally, I observed small green stems of *Asclepias speciosa* in the same region on October 21, 2024.

Figure 2.13: Native milkweeds during the late fall in the eastern Sierra Nevada in Mono and Inyo Counties. *Asclepias fascicularis* and *Asclepias speciosa* growing below Monitor Pass top left and center and along Twin Lakes on the top right and along Highway 395 near Walker, California on the bottom on October 20, 2023.

DISCUSSION

Discussion introduction

My central research question for chapter 2 was how do residential gardening practices influence the availability of milkweed vegetation during the winter months and how extensively is this vegetation used by winter breeding monarch butterflies? I further divided this question into four sub-questions.

Winter availability of milkweed vegetation

My first sub-question asked: How abundant is milkweed vegetation in urban gardens during the winter months and which species of milkweeds are most prevalent during the winter months? I found that milkweed vegetation was prevalent and readily available to monarchs throughout the winter. While the majority of this milkweed was *Asclepias curassavica*, *Gomphocarpus physocarpus* was common and a small amount of foliage on native milkweeds *Asclepias fascicularis* and *Asclepias speciosa* was also present. Additionally, I found that vegetation of *Gomphocarpus cancellata*, *Asclepias linaria*, and *Oxypetalum coeruleum* was available during the winter. I had predicted that milkweed vegetation would be common throughout the winter and that the majority of these plants would be *Asclepias curassavica.*

Winter maintenance of milkweed plants

My second sub-question asked: How are non-native milkweeds with active winter foliage maintained by gardeners? Do gardeners cut back milkweed plants during the winter and, if so, how much do they prune the plants? I found that most gardeners who cut back non-native milkweeds do so by the middle of January. Very few gardens that have green milkweed foliage that far into winter are subsequently cut back before the spring. Milkweed plants that have been pruned are meticulously pruned, often close to the ground, only leaving a small amount of foliage to support larvae that are close to pupating. Some gardeners cut back about half of their plants and not the others. Other gardeners, slightly prune the plants. I had predicted that milkweed vegetation management would vary greatly from garden to garden and that gardens would either contain plants that were all well-pruned closely to the ground removing the majority of leaves or not pruned at all with plants remaining similar sizes and shapes throughout the seasons and retaining leaves throughout the winter.

Many plants of *Asclepias curassavica* partially die back during the coldest and wettest portions of winter after being defoliated by monarch larvae in the late fall (personal observations). Plants that had been heavily infested by aphids during the late fall often were covered with aphid honeydew and sooty mold (personal observations, unpublished data collected on plant health during 2020 survey). Some gardeners pruned such plants slightly, but I suspect that this pruning was related to general spring garden preparation rather than intentional pruning to meet the recommendations of monarch conservation outreach. There was some variation in plants that were not cut back at all during the winter. Some plants did not appear to receive any maintenance during the year or from year to year. Interestingly, such gardens could often be located in close proximity to gardens that were meticulously maintained.

Although I could not include a social study of these dynamics including interviews and surveys for reasons detailed in Chapter 1, my general observations suggest that growing *Asclepias curassavica* is a contentious subject in the region. This may have been fueled by the banning of the sale of *Asclepias curassavica* in Marin County. News articles and signage often do not include citations and citizens appear to be communicating the directives without knowing details of the logic surrounding the directives. Many gardeners report being criticized for growing the plant at all even when they prune and care for the plants carefully and devote their properties to pollinator habitat. A non-scientist man told me that I should not have any milkweeds at all and that I should only have nectar flowers because I lived within 5 miles of the coast, despite him knowing that I was studying this system for my dissertation. After searching, I could not locate a citation for this recommendation. Other community members have pointed out that, given that we can literally see an overwintering site from our homes, it feels odd to suggest that our milkweeds would prevent migration to an overwintering site. As mentioned in Chapter 1, directives to the public should be specific to the area, explained fully, and cited to maintain public credibility and trust.

Winter use of milkweeds by monarch butterflies

My third sub-question asked: How prevalent is year-round breeding on non-native milkweeds that are not cut back during the winter? I found that monarchs actively utilize milkweeds throughout the winter. Early winter sees a large number of larvae that have escaped the high predation pressure of late summer (see Chapter 3 of this manuscript) and that continue to feed and pupate. Late January and early February see fewer larvae and egg numbers rise dramatically in March. High densities of eggs are common on plants and show a pattern of urban egg loading that has been documented in other urban areas (Baker & Potter 2020; James *et al.* 2021). I had predicted that monarch eggs, larvae, and adults would remain common throughout the winter and that adults would continue to oviposit on new growth. While winter monarch breeding in the San Francisco Bay Area has been increasingly recognized in scientific literature (Crone & Schultz 2021; James 2024; James *et al.* 2021; Schaefer & James 2024), winter breeding has been occurring in the region for many years (personal observations, Figure 2.14).

Figure 2.14: Monarch larvae on *Asclepias curassavica* on December 5, 2019, in Berkeley, CA.

Late fall and winter dormancy of native milkweeds

My fourth sub-question was: Do native milkweeds truly die back during the winter months? I had predicted that native milkweeds would die back fully during the winter months. However, I found that native milkweeds retained green vegetation that was actively utilized by monarchs well into the late fall for both *Asclepias fascicularis* and *Asclepias speciosa*. Additionally, some plants of *Asclepias fascicularis* remained green throughout the winter over multiple years. An underlying assumption of the arguments against non-native milkweeds is the idea that native milkweeds die back in the winter. While this is the general rule, my extensive field work has demonstrated that this is not always the case.

Many of the *Asclepias fascicularis* plants that remained green outside throughout the year in the larger study region were in protected areas that may have benefited from microclimates created by structures. Some structures likely provided physical protection in the form of fences and buildings and also heat radiating from building interiors. Other areas appeared to be near underground industrial equipment which may have provided heat from underground steam heating or mechanical operations potentially combined with increased heat output from higher coverage with impervious surfaces. I considered the possibility that plants could have been hybrids with other species but rejected this consideration after reviewing floral morphology and the likelihood of other species being obtained and planted in the sites.

In greenhouse grown populations of *A. speciosa* and *A. fascicularis*, most plants of *A. speciosa* died back during the winter months and resprouted in the spring. Given that plants did not receive artificial lighting and temperatures remained relatively constant, this suggests that plants of *A. speciosa* are responding to changes in photoperiod. Plants of *Asclepias speciosa* died back in the winter when grown under natural lighting reflecting a decreasing photoperiod suggesting that photoperiod is an important cue to trigger and brake dormancy even when grown at temperatures above outside temperatures. However, the majority of plants grown from seed in my greenhouse population of *Asclepias fascicularis* in the same room did not die back during the winter, leading me to believe that temperature is the main cue triggering and breaking dormancy for *Asclepias fascicularis*. Seeds for these *Asclepias fascicularis* plants came from two sources – one source was from a green strip grown plant still retaining its identifying tag from the source nursery and the other was from plants growing in a campus garden as described in the results.

It is also possible that the variation in winter responses reflects natural variation between populations *of A. fascicularis*. Studies have shown wide variation in seed germination needs between populations of the same milkweed species without any pattern in latitude in some studies (Bandara *et al.* 2019; Kaye *et al.* 2018; Landis & Dumroese 2015; Luna & Dumroese 2013). It is possible that nurseries unintentionally favor populations that more readily germinate and that appear more attractive to consumers throughout the year. Understanding how plants from different populations might respond to temperature changes is important to plan for climate change and to retain diversity in commercially available plants (Bandara *et al.* 2019).

However, this finding of *A. fascicularis* growing throughout the winter should not lead to a recommendation that gardeners plant *A. speciosa* instead. I documented some plants of *A. speciosa* that were also green in mid-January of 2021 and others that were green in early December of 2023. Additionally, in my four years of observations, I have consistently found large stems of *A. speciosa* without signs of larval herbivory while other species of milkweeds had larvae. Adult monarchs would oviposit on newly sprouting *A. speciosa* in the spring and on new growth but would seemingly ignore mature foliage. I suspect that this pattern may be in part the result of high trichome density and high amounts of latex in leaves of *A. speciosa* often grown in these gardens. Local nurseries have sold a cultivar of *A. speciosa* called "Davis" and this cultivar has unusually hairy leaves. Gardeners love the foliage, but monarch larvae do not appear to favor it.

Additionally, travel throughout northern California during autumn leads me to believe that native milkweeds are often green late into the fall. Mid-October travel to a reserve near Willits in Mendocino, California and late-October travel to the eastern Sierra Nevada in Mono and Inyo counties also lead me to believe that these species of milkweeds often remain green into late fall. I began noticing milkweed plants along mountain highways in these counties in recent years but did not recall seeing them in my previous two decades of travel in the region which often took place in late August through October. I have suspected that these plants may have originated from seed balls distributed by well-intentioned citizens due to their close proximity to pavement on highways. However, a wildlife biologist colleague with 15 years of extensive field experience in northern California also reported to me that he had increasingly observed monarchs at higher elevations and in regions where he had not previously seen the butterflies (personal communication with Ryan Byrnes).

Synthesis

In Chapter 2, I sought to better understand how milkweeds and monarch butterflies are interacting during the winters. Milkweed vegetation is abundant during the winter in this study region. Although some gardeners carefully prune their non-native milkweeds, the majority of gardeners do not prune their milkweed plants. Monarchs actively utilize milkweeds throughout the winter with monarch adults, eggs, and larvae present during all months. Early winter sees a large number of larvae close to pupation. Late January and early February see fewer larvae and egg numbers rise dramatically in March. High densities of eggs are common on plants and show a pattern of urban egg loading that has been documented in other urban areas (Baker & Potter 2020; James *et al.* 2021). While most of the winter use of milkweeds is on non-native milkweeds *Asclepias curassavica* and *Gomphocarpus physocarpus*, I have also observed winter monarch larvae feeding on *Gomphocarpus cancellata*. Additionally, many individual plants of native milkweeds *Asclepias fascicularis* and *Asclepias speciosa* are retaining green vegetation through all or part of the winter. These plants are from different seed and nursery sources, are found in different locations, and can remain green during multiple winters.

There are concerns that non-native milkweeds will cue monarch butterflies to breed during the winter when they might otherwise overwinter at roosting sites along coastal California and that larvae will be exposed to higher levels of the *OE* parasite as the spores accumulate on foliage that remains green year-round. Some scientists and conservationists are concerned that these resident monarchs might fail to migrate and might harm monarchs that do migrate. Other experts believe that climate change is the primary cause of winter breeding.

It is important to remember that there are real consequences to the way in which the public receives information about milkweed. One individual told me that they would actively smash monarch eggs oviposited on their milkweed during the winter because they were not supposed to be active then and the subsequent monarchs could be harmful (identity and garden excluded from study to protect privacy). A post on the social media site Nextdoor reported that someone had witnessed a person picking things off of a milkweed plant and smashing them with their feet on the sidewalk and that the poster was concerned that these things were winter monarch larvae (posted widely such that the communication would be reasonably construed as public). While I could not verify this report, it would also not surprise me. Monarch larvae in cold temperatures often display darker coloration and display comparatively sluggish behavior (Davis *et al.* 2005) which I suspect could lead a person to believe that the larvae were ill.

Limitations and future directions

Limitations

Despite limitations in my study design, the data that I collected includes rare observations from this region before and during the crash in the western monarch population which occurred during the winter of 2020 - 2021. My study also did not intend to extrapolate to scaled up regional monarch counts. I intended to document phenomena that have been occurring and that may be early signals of larger trends.

Future directions

Future studies should conduct regular counts of monarch larvae and eggs in a more systematic manner. However, doing so will present many challenges because the system is inextricably tied to human behavior. People regularly move monarch larvae across the landscape when their own milkweed plants have become completely defoliated (personal observations and online public forums) often because gardeners cannot trust nursery plants to truly be pesticide free (Halsch *et al.* 2020, 2022). A large aggregation of monarch larvae may simply represent the re-location of all of the larvae in a garden to one plant to allow the other plants to be cut back. An aggregation could also represent a neighbor moving hungry larvae to a plant on a different block or across the city. Controlling for these human actions is difficult. More controlled environments such as those in a gated campus garden might be easier to control, but they can cease to represent the rest of the naturally dynamic urban landscape. Controlling for human interactions with monarch larvae can even be difficult in gated campus gardens. Such spaces are used by many students and researchers with many competing interests. Campus sites are also dynamic. One campus garden containing a small patch of native milkweed which was frequently utilized by monarch larvae suddenly disappeared after being bulldozed to build a new data science building on the main University of California Berkeley campus. Given the dynamic qualities of urban spaces, future research should also consider mixed ecological and social science methods to obtain direct information on what is happening in each garden.

Broader implications

If native milkweeds are remaining green and monarchs are using them, critics of non-native milkweeds must consider the role of climate change in the patterns that they observe. Extreme winter storms have also impacted overwintering colonies. The early days of my surveys were during the extreme fire season of 2020. I would argue that our climate is not the climate of the 1980s and 1990s and it is not surprising if milkweeds are changing their phenology and that monarchs are also responding to these changes. I think that there is a case to be made for considering all of the tools in our toolbox including non-native milkweeds and monarchs that might not fit our perception of what is natural. If some native milkweeds are dying back later in the fall or staying green throughout the winter, is the solution to not grow native milkweeds as well or to seek out populations of milkweeds that die back earlier? Should milkweeds growing in the regional parks of the east bay hills be culled? At some point such efforts are fighting to restore landscapes and phenological patterns to historical timepoints that no longer reflect today's realities.

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Chapter 3: Something gobbled up my caterpillars! Predators and predation patterns impacting monarch larvae in urban gardens of the Bay Area

ABSTRACT

Despite their unpalatable reputation, predation on monarchs is surprisingly high. Only a small percentage of monarch eggs will go on to become adult butterflies. While predation is high, identifying which predators have consumed monarch eggs and larvae can be surprisingly difficult. My study sought to formally document common predators of monarch larvae in urban gardens in the San Francisco Bay Area. From the summer of 2021 through the fall of 2024, I recorded all observed fatalities of monarch larvae in a set of experimental gardens. Additionally, I conducted structured predation trials in field conditions to assess predator diversity and pressure on third through fifth instar larvae. Almost all documented monarch fatalities were caused by predation by the invasive European paper wasp (*Polistes dominula*). During extended day and nighttime observations, I observed two species of vertebrate predators consuming monarch larvae. I observed one event, using a motion detection video camera, of a scrub jay (*Aphelocoma californica*) consuming a single fifth instar larva. I also recorded a dusky-footed wood rat (*Neotoma fuscipes*) removing milkweed branches and appearing to consume multiple larvae over the course of two nights using a motion detecting night vision video camera. Other species documented attacking or consuming monarch larvae were yellow sac spiders (*Cheiracanthium* spp.), Argentine ants (*Linepithema humile*), and yellow jackets (*Vespula pensylvanica*). Attacks by *Polistes dominula* wasps would sometimes result in monarch larvae dropping from plants and escaping into dense ground cover or weedy vegetation around plants. However, most attacks were fatal and resulted in larvae being skinned, gutted, dismembered, and delivered to wasp nests. Wasps would return for repeated trips until only larval gut matter and head capsules remained. *Polistes dominula* wasps would continue to attack and kill larvae on experimental plants until all larvae had been killed. These high fatality days generally occurred on hot days in the late summer. Attacks were almost always mounted by a single wasp that had encountered the plant. In earlier summer trials, attacks were less common on monarch larvae in two gardens dominated by agricultural plants despite the wasps being ubiquitous in those gardens. *Polistes dominula* on these days could often be seen hunting along crops in the Brassicaceae, potentially searching for lepidopteran larvae of other species. *Polistes dominula* nests were often difficult to locate or access, with several large colonies found in a dilapidated power pole and cable box. By mid-October, *Polistes dominula* ignored monarch larvae even on days with high wasp activity on unseasonably hot days suggesting that colonies were no longer provisioning larvae and were preparing for overwintering locations. No commercially available traps were able to capture *Polistes dominula*, consistent with findings from other studies. Climate change is likely to be highly beneficial to this species of invasive wasp in the study area, likely increasing larval monarch mortality. During times of peak *Polistes dominula* activity, monarch larvae were rare on plants in the study area, suggesting that this one invasive species is a great threat to larvae. Future efforts should focus on control of the wasp and working with property owners to locate wasp nests early each season. Indoor rearing of monarch larvae in the region is likely due to gardeners attempting to protect their larvae from being consumed by this invasive wasp.

INTRODUCTION

Despite their reputation as unpalatable due to sequestration of chemical defenses obtained from their diet of milkweed, predation on monarch butterfly eggs and larvae is actually quite high. As is common with many species of Lepidoptera, only a small percentage of monarch eggs live to become adults (Borkin 1982; De Anda & Oberhauser 2015; Oberhauser *et al.* 2001; Zalucki & Kitching 1982). One observational study found that only 20% of monarch eggs survive to become first instar larvae, while less than 10% live to become second instars and only less than 2% survive to become third instars (De Anda & Oberhauser 2015). Earlier studies estimated the survivorship of monarch egg to pupation as 12% (Borkin 1982) and from egg to fifth instar as 2-8% (Borkin 1982; Zalucki & Kitching 1982). While studies consistently find that few monarch eggs live to become adults, the fate of each egg and larva is much more elusive. Many studies report that larvae simply disappear (De Anda & Oberhauser 2015) and it is common that only small numbers of predation events are observed in field settings even during long-term studies (De Anda & Oberhauser 2015).

While egg and larval fatality rates are clearly high, it can be more difficult to identify the actual predators of monarchs and the environmental conditions likely to lead to higher predation rates. Laboratory experiments have revealed additional information on the identities of larval and egg predators. Some insects commonly used in biocontrol have been found to consume monarch eggs or larvae. One study found that lacewing (*Chrysoperla rufilabris*) larvae reared on frozen Mediterranean flour moth (*Ephestia kuehniella*) eggs up until the third instar readily consumed monarch eggs when other food sources were not available (Oberhauser *et al.* 2015). When both field and laboratory studies are combined throughout all regions colonized by monarchs, the list of possible predators spans many taxa. Documented predators of at least one life history stage of monarchs include species of lacewings, ants (*Formica montana*, fire ants), beetles (*Harmonia axyridis* and some species of Coccinellidae), pentatomid nymphs, mantids, some spiders, some dragonflies, birds, mice, and multiple species of wasps (Hermann *et al.* 2019; Hudman *et al.* 2023; Koch *et al.* 2006; Oberhauser *et al.* 2015; Rafter *et al.* 2013; Rayor 2004). Studies and observations up until 2015, were well reviewed and organized by study location and predator by Oberhauser *et al*. (Oberhauser *et al.* 2015). Suffice to say; the world is a dangerous place for a little caterpillar.

The majority of previous studies on predation of monarch eggs and larvae have focused on predation patterns in rural locations in the eastern and mid-western United States. Previous studies have also focused on natural areas that often include higher arthropod diversity with comparatively fewer studies in urban and suburban systems. However, larvae in some urban areas have been shown to experience higher predation rates by an invasive wasp *P. dominula* (Baker & Potter 2020). Additionally, most of these studies have been conducted on milkweeds native to the eastern United States with predators common to that region. There is less information on the potential predators impacting monarch butterfly larvae in the western United States.

As is common with early ecological observations, people living and working in landscapes often note changes in ecological communities and share that information. Bay area gardeners are well aware of the high larval predation rates on their properties. Some gardeners have identified wasps as a main predator (personal communications with gardeners). Others have suspected various spiders and birds (personal communications with gardeners). These suspicions can be problematic as few people can identify wasps to species and gardeners may be tempted to kill all suspected predators including those that might be beneficial (personal communications with gardeners). Gathering locally relevant information on monarch predators could help inform general insect conservation outreach to the public. This type of outreach could potentially minimize the chances of gardeners killing beneficial wasps and spiders that do not eat larvae. Property owners could also learn how to identify invasive predators and their nests early each season. It is also important to predict which predators may do better under future climate change conditions and which tools do and do not help target those predators.

Objectives and Questions

I divided my study into two parts. In the first part, I sought to identify the primary predators impacting monarch butterfly larvae in urban gardens of the East Bay. After identifying common predators of monarch larvae in the system and determining the predators responsible for the most larval fatalities, I sought to better understand the factors influencing predation pressure and success of these predator species. In the second part of my study, I investigated the factors influencing predation pressure and success of the invasive European paper wasp *Polistes dominula*.

Part 1: Identification of predators of monarch larvae in urban gardens of the East Bay

My central research question for Part 1 of Chapter 3 was: What are the primary predators of monarch butterfly larvae in urban gardens of the East Bay?

Part 2: Factors influencing predation pressure and fatality of attacks by Polistes dominula wasps on monarch larvae

My central research question for Part 2 of Chapter 3 was: Which factors influence predation pressure and success of the invasive wasp *Polistes dominula*? My sub-questions for Part 2 were:

1. How do temperature and periods of extended high temperatures impact predation by *Polistes dominula*?
2. Can higher than average daily temperatures or multi-day heat waves predict the number of *Polistes dominula* attacks or the fatality of those attacks?
3. How does the local plant and insect community in a garden impact predation by *Polistes dominula* on monarch larvae?

Predictions

Part 1: Identification of predators of monarch larvae in urban gardens of the East Bay

I predicted that:

1. Predators would be diverse, but that the primary invertebrate predators would be both native and non-native wasps. I also predicted that *Polistes dominula* would be the primary invertebrate predator of larger monarch larvae. I also expected that invasive rats and some birds would consume monarch larvae and that ants and spiders would prey upon younger larvae.
2. European paper wasps, *Polistes dominula*, would be extremely effective larval predators with almost all attacks leading to fatality. Monarch larvae would respond to attacks by thrashing their heads, dropping by silk, or rolling into balls and dropping to lower leaves or the ground. Additionally, larvae close to the ground or in large, structurally complex plants would be most likely to survive predators.

Part 2: Factors influencing predation pressure and fatality of attacks of Polistes dominula wasps on monarch larvae

After observations and predation trials in Part 1, I predicted that predation pressure and attack fatality rates of monarch larvae by *Polistes dominula* would be high, but would vary due to season, temperatures, and the presence of host plants potentially supporting more palatable species of Lepidoptera larvae. Specifically, I predicted that:

1. High temperatures and periods of extended heat would increase the predation pressure and likelihood of fatal attacks. Based on the published reproductive physiology and temperature responses (Cervo *et al.* 2000; Käfer *et al.* 2015; Kovac *et al.* 2023; Liebert *et al.* 2006; Weiner *et al.* 2011) of *Polistes dominula*, I postulated that increased temperatures would decrease the developmental time of *Polistes dominula* larvae, requiring adults, which are progressive provisioners, to increase their predation rate.
2. Gardens with abundant insect food sources, particularly lepidopteran larvae, would have lower monarch predation as wasps could choose to select more palatable prey. As more palatable prey are consumed and become a less consistent resource, wasps would increasingly attack less palatable prey such as monarch larvae. Wasps with fewer resources would mount more aggressive and prolonged attacks of larger monarch larvae and would be less likely to be deterred by defensive strategies of larvae, resulting in attacks becoming more fatal.

METHODS

Study area

Regional landscape

My larger study focused on the residential monarch butterfly population in the East Bay of the San Francisco Bay Area and the milkweed gardens in that region (Figure 3.1). My study focused on two areas within this larger region (Figure 3.2). The first area was a primarily residential neighborhood east of a monarch overwintering site on Albany Hill. This neighborhood includes portions of the cities of Berkeley, Albany, El Cerrito, and Kensington, California. Elevations range from 14 meters above sea level just above the San Francisco Bay to approximately 150 meters above sea level in the hills below Tilden and Wildcat Canyon

Regional Parks. The site includes retail and business properties concentrated along main streets, multiple smaller parks, schools, and a large regional cemetery. Most of the properties are single family homes owned by the residents who occupy those homes. Green strips, strips of public land located between a sidewalk and a road and maintained by adjacent property owners, are present on both sides of most streets but vary in width from city to city. Green strips also vary in the amounts of impervious surfaces such as concrete and in cultivation practices. Lot size and structure placement in lots are relatively uniform in El Cerrito and Albany but differ greatly in higher elevation Berkeley and Kensington. The southwestern portion of this area is also near the University of California Berkeley Gill Tract Farm with another recently documented monarch overwintering population (Xerces 2024). The second area includes the main campus of the University of California Berkeley, the Oxford Tract agricultural field, student gardens, pollinator gardens, and residential lots.

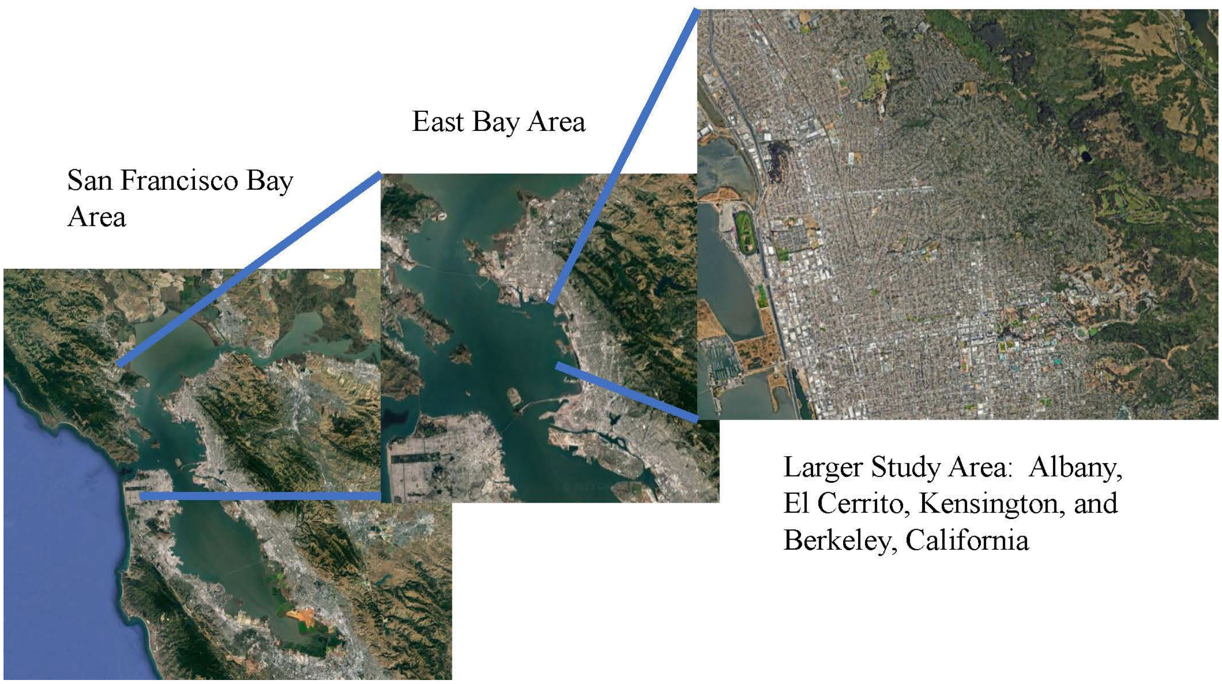

Figure 3.1: Map of study area. A map of the greater San Francisco Bay Area in California showing the larger study area in greater detail (Google Earth 2024).

Figure 3.2: Yellow diamonds indicate the two documented overwintering sites in the immediate area. Orange stars indicate the general locations of study gardens. Exact locations of the residential study gardens are not included to protect gardener privacy.

Regional climate

This region has a temperate warm summer Mediterranean climate, Köppen-Geiger climate zone Csb (Beck *et al.* 2018, 2023), characterized by wet, cool winters and warm, dry summers. The highest temperatures of the year are often in September and even into early October. Traditional summer months of June, July, and August are influenced by the coastal fog belt and mornings can be cool and cloudy up until 12 noon or later in the day when the fog layers burn off. Temperatures can vary greatly day to day and nighttime temperatures are lower than daytime. There can also be considerable fine scale micro-climate differences which impact growing conditions (Carpenter & Rosenthal 2011; Peirce 2010). The region has a climate that is very different from many other regions that host monarch butterflies. These unique climatic characteristics influence the growth of milkweed and the times of highest insect activity during the year and during the day. It is common to have days with temperatures over 27 degrees Celsius and even over 32 degrees Celsius well into the end of October. Consequently, plants are still in full growth in the fall. Butterfly activity in the region also peaks in the late summer through the early fall (Shapiro & Manolis 2007).

Larger study system: Northeastern San Francisco Bay urban monarchs and milkweed gardens

History and conservation of Western monarch population and near-by overwintering sites

While discourse surrounding monarch butterflies has historically focused on the eastern North American population which overwinters in Mexico, written records of monarchs overwintering in costal California date back to the late 1800s (Anonymous 1874; Bush 1881; Lane 1993; Thaxter 1880; Vane-Wright 1993). Regular annual counts of overwintering monarch butterflies in California began in 1997 (Malcolm 2018; Xerces Society Western Monarch Count 2024). These counts have shown a dramatic decline since 1997 and high variation between years (Xerces Society Western Monarch Count 2024). Some estimates speculate that counts during the 1980s were much higher with at least 4.5 million butterflies (Schultz *et al.* 2017). The monarch population faces many threats (Crone & Schultz 2021; Jepsen & Black 2015; Malcolm 2018; Pelton *et al.* 2019; Schultz *et al.* 2017) which I also detail in Chapters 1 and 2 of this manuscript. Two overwintering sites are located in this larger study area (Xerces Society Western Monarch Count 2024). Research and conservation interest in the Bay Area population of monarchs has increased after the record low winter count of overwintering western monarchs (Crone & Schultz 2021; James *et al.* 2021; Schaefer & James 2024).

Distribution, species composition, abundance, and winter availability of milkweed species

Residential cultivation of milkweed is common and is growing in popularity, however very few species are commonly grown in this area. Only four species of milkweeds are regularly encountered in local residential gardens: *Asclepias curassavica*, *Asclepias fascicularis*, *Asclepias speciosa*, and *Gomphocarpus physocarpus*. Species rarely encountered include: *Gomphocarpus cancellata*, *Asclepias incarnata*, *Asclepias tuberosa, Asclepias linaria*, and *Oxypetalum coeruleum* (Chapter 1 of this manuscript). Species descriptions can be found in resources cited in the references section (Borders & Lee-Mäder 2014; Borders & Mader 2011; Motooka 2003; Singhurst *et al.* 2015)

Identification of predators of monarch larvae in urban gardens of the East Bay

Summary

I analyzed the patterns of monarch larvae predation in urban gardens using a mixture of direct observation, videos, and structured predation trials in multiple residential and campus gardens during 2021, 2022, and 2023. After combining these observations, I determined which predator species resulted in the highest number of monarch larvae fatalities. I also identified species responsible for non-fatal attacks and for encounters that resulted in larvae making visible physical responses.

Study garden selection and characteristics

To best represent the habitat of the region, I selected locations in private residential gardens, in green strips, and in larger publicly accessible gardens (Figure 3.3). To represent the plant communities that were present in the larger system, I selected gardens with similar plant species and recorded the plants present to the finest taxonomic level possible. To identify possible wasp nests, I walked the perimeter of each garden on the first day of observation. I checked the eves of all structures in the gardens including sheds and also examined open pipes, wooden structures (such as composting bins and potting tables), benches and chairs, any playground equipment, and any bird houses for evidence of wasp nests. When privacy and access permitted, I also scanned adjacent lots for wasp nests with binoculars. I recorded any evidence of current or past nests.

Figure 3.3: Examples of one study garden located in a campus pollinator garden in a green strip.

Predation trials

Milkweed sourcing and cultivation

To provide experimental larvae for the predation trials with a standardized food source free from pesticides and *Ophryocystis elektroscirrha* (*OE*) spores, I grew milkweed plants in greenhouse conditions from seeds harvested from plants within the study system. To minimize variation in herbivore-induced host plant chemistry and other nutritional traits, I reared larvae on cuttings from designated plants in this standardized population of milkweed plants which had not been fed upon by monarch larvae (in that growth season). Studies have found considerable within species variation in cardenolide chemical concentrations and other measures of plant quality (Agrawal *et al.* 2015). While it was not possible to use clones from rhizome cuttings, I minimized variation in host-plant traits by using seeds from individual milkweed stands.

Seed sourcing and collection

I harvested seeds collected from residential gardens in the study area during the fall of 2020 and the fall of 2021. I collected seeds of the four species of milkweeds that were most common in the study area: *Asclepias fascicularis*, *Asclepias speciosa*, *Asclepias curassavica*, and *Gomphocarpus physocarpus* (Chapter 1 of this manuscript). I selected plants that I suspected to be source plants of many volunteer plants in neighboring lots. I also selected plants that supported larvae in previous observations and for which I could gain access and permission (Chapters 1 and 2 of this manuscript). I initially collected seeds on dry days in envelops and stored the envelops in a cool dry location away from direct sunlight for further sorting. I separated seeds from the attached floss using a zip lock bag method that has been used by others (Landis & Dumroese 2015), separated out smallest seeds, and repackaged seeds in a seed archive.

Seed cleaning and germination

To decrease the chances of contamination, I cleaned all seeds in a dilute bleach solution before germinating seeds. I used a solution of 5% bleach and 95% distilled water. I rinsed seeds from each plant in the bleach solution for 1 minute while swirling the container for even coverage. I then strained seeds from the bleach solution, rinsed seeds with distilled water, and re-strained seeds. While most studies utilize cold moist stratification to germinate native milkweed seeds (Borders & Lee-Mäder 2014) variation in germination needs can vary greatly between populations of the same species of milkweed (Bandara *et al.* 2019; Kaye *et al.* 2018). Reports from online gardening forums and personal observations indicate that many native milkweeds will readily germinate after being soaked in water without the extended cold moist treatment. I soaked seeds in distilled water at ambient room temperature away from direct sunlight until 1 or more seeds formed a root tip. After seeds began to germinate, I transferred each batch to a plastic storage container lined with a clean paper towel.

Seedling transplanting and cultivation

I placed each germinating seed in one cell of a 6-cell pot filled with professional grade grade high drainage potting aggregate (Sunshine Mix #4 Professional Growing mix; composition: Canadian *Sphagnum* peat moss, perlite, Dolomite lime, and wetting agent), covered seeds with a thin layer of the same aggregate, placed each 6-cell pack in a flat tray with drainage holes, watered germinating seeds with municipal tap water (East Bay Municipal Utility District), and placed flats in a room at the University of California Berkeley Oxford Tract Facility Greenhouse. I planted the seeds in July of 2022. The greenhouse room temperature generally ranged from lows of 18 degrees Celsius to highs of 24 degrees Celsius with a natural photoperiod and no additional artificial light. To decrease the possibility of root rot during winter dormancy, I potted up growing seedlings into a mixture of 2 parts Sunshine Mix #4 to 1 part perlite into 4-inch pots. I periodically fertilized all plants with a solution of algae-based all-purpose fertilizer (Maxsea Brand 16-16-16). As plants grew larger, I potted up the plants to 4 inch then 1-gallon pots using the same ratio of 2 parts Sunshine Mix #4 to 1 part perlite. On March 2, 2023, the vendor supplying potting materials to the facility was no longer able to to supply Sunshine Mix #4 without additives. This mix was replaced with a substantially similar high drainage potting aggregate (Lambert LM-6 High Porosity Mix, composition: extra coarse Canadian *Sphagnum* peat moss (75-85%), coarse horticultural perlite, calcitic limestone, Dolomitic limestone, wetting agent, and starter charge).

Greenhouse-grown milkweed pest management

To minimize any herbivore-induced variation of plant secondary chemistry while also not using any pesticides, I used a mixture of mechanical pest removal, pest trapping, and purchased and natural biocontrol. While I made every effort to protect greenhouse-grown milkweed plants from herbivores, several common greenhouse pests did attack plants during 2022 to 2023, likely entering from other greenhouse rooms. These included a small infestation of aphids (*Aphis*), spider mites (Tetranychidae), greenhouse thrips (Thysanoptera), and fungus gnats (Sciaridae). No insect specialists of milkweed fed on the greenhouse-grown milkweed plants prior to them being given to experimental larvae. I manually removed aphids by hand-washing leaves in a dilute solution of mild soap (Second Generation brand) and tap water followed by rinsing off the soapy solution from leaves with tap water. I also set yellow and blue sticky traps (Seabright Laboratories) throughout the plants on each greenhouse bench to decrease populations of aphids, fungus gnats, and thrips, and to monitor for pests in general. Oleander aphids (*Aphis nerii*) are abundant on milkweed plants in outdoor gardens adjacent to the greenhouse facility and attract multiple species of coccinellid beetles and aphid-specialist parasitoid wasps. I also captured and released these coccinellid beetles and adult wasps reared from outdoor mummies to control aphid populations. Additionally, I released commercial biocontrol mites to manage populations of greenhouse thrips (*Amblyseius cucumeris*, *Amblyseius*-System, Biobest Sustainable Crop Management; immediate release system in a bran carrier and extended-release sachets) and spider mites (*Neoseiulus californicus*, *Californicus* Breeding System, Biobest Sustainable Crop Management, sachets). Pest prevalence was evenly distributed through the room.

Egg sourcing and rearing of experimental larvae

I reared each experimental larva for the predation trials from the egg stage in a separate, clean plastic deli container. I harvested wild monarch eggs from designated egg collection plants in a private residential urban garden (CDFW SCP S-230290001-23074-001). I made every attempt to harvest newly oviposited eggs from new foliage to decrease the chances of egg surfaces coming into contact with *OE* spores deposited by adult butterflies. I removed eggs from the original plant material and transferred each egg to a clean plastic polypropylene deli container (size 3.5 oz, EDI brand) with a leaf cutting of the desired milkweed species. While I had grown plants from seeds of the four milkweed species referenced above to allow for trials with all four species, various factors limited the larvae available for predation trials and I focused this portion of my study on *Asclepias fascicularis*.

Oviposition began later in the summer of 2023 than I had observed in the summers of 2020, 2021, 2022, and 2024 (personal observations). Eggs were less abundant and less densely clustered and many native milkweed plants emerged later in the spring that year (personal observation). The scarcity of eggs was reported to me by multiple gardeners throughout the region who had contacted me by email to ask if this pattern was observed by others. The paucity and lateness of eggs required that I exercise extreme care with the eggs that I could harvest. Due to these constraints, I did not treat eggs with a bleach solution to avoid potential loss of eggs through the handling and cleaning process. As an alternative, I regularly replaced egg collection plants with new plants not previously exposed to monarchs to decrease the chances of *OE* spore deposition by previously visiting adult butterflies.

To prevent cross contamination in the rearing population, I only used containers that were new and unused or containers that had been triple cleaned by rinsing in a separate room, soaking in a 20% bleach solution, and thoroughly rinsing. If any larva displayed unusually sluggish behavior, I immediately separated the larva in its individual container. As larvae grew, I replaced cuttings with fresh cuttings, removed frass, and moved larvae to larger containers. If a container was noticeably soiled after removing frass, I replaced it with a clean container. I generally kept neonates in a 3 to 4.5 oz. closed plastic deli container (EDI brand) and moved first and second instar larvae into 4.5 oz containers if they started in 3 oz containers.

I moved larger larvae into 16 oz plastic deli containers (Stackman brand) with a custom-made ventilated lid consisting of fiberglass window screen covering an opening in the plastic lid (standard deli container lid with a disc of plastic removed from the center and covered with a slightly larger disk of fiberglass window screen attached to the plastic lid with hot glue gun glue). I moved larger fourth instar and fifth instar larvae to 32 oz containers using the same lid. To prevent milkweed cuttings from wilting, I covered the ends of small clippings with organic cotton balls dipped in tap water. I placed larger milkweed cuttings in small plastic floral tubes.

To balance the need to keep larvae at the same environmental conditions while also preventing any stress from overcrowding, I stored the containers in 3-tiered plastic cabinets (Brightroom brand 3-drawer carts). This set up also allowed me to rapidly quarantine any sick larvae and adjacent containers if illness occurred. The plastic material of the cabinets was easy to disinfect with soaking or spraying down the containers with a 20% bleach solution. I placed the shelving in one of the two milkweed greenhouse rooms with natural light, but not in direct sunlight. The room was only exposed to natural light and the photoperiod of the natural environment outside. The room had a cooling system to prevent overheating common in greenhouses and generally fell in the range of 18 degrees Celsius nighttime lows to 24 degrees Celsius daytime highs. All larvae that were not consumed by naturally occurring predators during predation trials were reared to adults after the trial and tested for *OE* with either scotch tape or clear envelop sealing tape circles (Avery 5248) (Altizer 2023) attached to slides and viewed under magnification before being released per permit stipulations.

Presentation plant selection

To minimize the variables of plant growth habit, chemistry, and trichome density, I conducted the vast majority of predation trials with one milkweed species - *Asclepias fascicularis*. I utilized larvae that had been reared on *Asclepias fascicularis* vegetation from the same seed source as the presentation plants. I conducted a small number of additional trials utilizing *Asclepias curassavica* and *Asclepias speciosa*, with larvae that had been reared on the respective species. To minimize the potential impact of plant structure on predation, I chose plants that were structurally similar to each other for every trial. Presentation plants were the same age (grown from seed during July 2022 and no flowers present at the time of trial), the same size (1-gallon pots), grown in the same conditions, and were not exposed to herbivory by monarchs or other milkweed specialists in the growing season used.

Selection, acclimation, and placement of experimental larvae

Given the restrictions surrounding monarchs in California, my rearing population was limited. I primarily focused on larger instars in part because it was difficult to follow second and first instar larvae in video trials due to movements of leaves relative to the depth of field of macro video. Observing these interactions by binoculars was also not practical for the large ranges of time that might exist between predation events. For these reasons, I conducted structured predation trials with third, fourth, and fifth instar larvae. I chose the larvae for each predation trial based on what was available on a trial date after avoiding larvae nearing molting or pupation.

I placed five experimental larvae onto a standardized presentation plant and allowed the larvae to acclimate and move freely on the plant in an indoor environment protected from predators. While most of the larvae settled on the plant in the first 15 minutes, I extended the duration of the acclimation period to at least 60 minutes to allow comparison to previous studies in other regions (Baker & Potter 2020). I followed best practices to minimize the impact of handling on larvae (Davis 2020). Given that plants can release predator attracting volatile organic compounds in response to herbivory (Thaler 1999), I conducted the acclimation period away from the experimental site typically inside a greenhouse for trials on the University of California Berkeley campus and inside a private residence for trials off-campus. After the 60 minutes, I transported the plant and larvae carefully to the experimental site, typically by hand. For two sites with a smaller number of trials, I had to transport the plant with larvae in a vehicle for 2 to 3 blocks and then walk the plant to the site. I balanced the need to have larvae acclimate in a consistent environment with the realities of a highly urbanized area. I selected the garden site for a particular date based on the access restrictions of a site.

While a density of five larvae per plant is higher than what is documented in many field conditions (Borkin 1982), five larvae on a plant represents the highest density that I have personally observed on some plants of similar sizes in the study system. Monarchs in urban environments have been documented depositing large numbers of eggs on one plant or in a small area both in this region (personal observations, Chapter 2 of this manuscript) and in other regions (Baker & Potter 2020; James *et al.* 2021). I have also observed monarch larvae at this density on isolated plants, during late summer or early fall when larvae may move from defoliated plants in a patch and cluster on one plant with the most remaining foliage (personal observations). This increase in larval density can also be seen during some warm late falls and early winters (personal observation in the study system and in a restored field in Willits, Mendocino County, California).

Video recording of predation trials

I utilized a portable Gopro camera (Gopro Hero 9) video recording set up to maximize frames per second, depth of field, and the ability to record insects in the surrounding vegetation while not losing focus on the experimental plant and larvae. This set up also allowed me to film in more locations without using a more conspicuous DSLR macro lens set up that can attract theft in field conditions in the region. To allow for extended recording, I employed an external power bank (Suptig Portable Power Bank, 7800 mAh lithium, 5V/2 A) connected to the Gopro and mounted the battery pack and camera on a lightweight tripod to maximize air flow and to prevent overheating shut offs commonly activated by camera firmware. I further extended video times in hot conditions and full sun, by mounting a small adjustable UV shade (Dreambaby Clip-on Sunshade) on to an adjacent secondary tripod. This two-tripod system allowed me to shield the camera from UV radiation and related overheating, maintain air flow, and allow for wind gusts which could move the shade without impacting the stability of the camera on the primary tripod (Figures 3.4 and 3.5). I generally filmed using 4K and 30 fps at 19 mm. To allow full view of the experimental presentation plant and all larvae, I adjusted the distance from the center of the pot to the center of the camera tripod to account for plant dimensions and the topography of the ground, but this distance generally ranged from between 70 to 90 cm. I made further adjustments in tripod leg length to balance the camera and battery pack when filming vertically. To provide a set-up that would be accessible and reproducible to citizen scientists, I made every attempt to use materials that could be purchased by, built, and accessible to the general public. For each trial, I recorded the plant with larvae in the study garden for at least 60 minutes. Whenever access and time allowed, I extended recordings to two to three hours. While at the trial location I recorded other insects in the garden visually (sometimes with binoculars) and with a separate camera at a distance to not disrupt the movements of those insects.

Figure 3.4: Camera field set up for predation trials in a residential garden and a residential green strip in the study area.

Figure 3.5: Camera field set up for predation trials in campus field and pollinator gardens. From left to right, the photos show set ups in a pollinator garden in a green strip, a pollinator garden on main campus, and a field that includes both pollinator plants and food crops.

Extended day and nighttime motion detection camera traps 2023

Given that vertebrate predators were less likely to approach larvae with a human observer present in the garden, I also set up a low-cost motion detecting camera for extended day and nighttime observations (WyzeCam v3 camera connected to Suptig Portable Power Bank). Due to the risks of theft in the gardens, I was only able to conduct these trials in one residential garden and in a gated lathe house adjacent to greenhouse facilities (daytime only).

Additional predator observations from 2021 through 2024

I also recorded detailed information of predation events observed in prior years to inform experimental design (unpublished data). While the details are not included in this study, I included the species that I directly observed killing or consuming monarch larvae throughout 2021 to 2024.

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Factors influencing *Polistes dominula* predation on monarch larvae

Temperature

I downloaded regional weather data for the trial days and compared that data with attack metrics such as number of attacks, number of fatal attacks, number of inspections, likelihood that an inspection leads to a fatality. This data is still being processed.

Plant communities and alternative food sources

I recorded plant species and insects present in each study garden to compare to attack and temperature data. This data is still being processed.

RESULTS

Identification of predators of monarch larvae in urban gardens of the East Bay

Daytime structured predation trials

During a total of over 50 hours of formal predation trial observations in 2023 between August through mid-October, all but one documented larval monarch fatality was caused by predation by invasive *Polistes dominula* wasps. Only one other species killed a monarch larva in these trials. On one instance, a yellow jacket (*Vespula pensylvanica*) repeatedly attacked a larva, resulting in the larva dying shortly after the trial, but the attacking *Vespula pensylvanica* did not consume the larva.

Extended day and nighttime motion detection camera traps 2023

During extended day and nighttime observations, I observed two species of vertebrate predators consuming monarch larvae. On September 29, 2023, I observed a scrub jay (*Aphelocoma californica*) consume one fifth instar monarch larva (Figure 3.6). Using the same camera system on night vision mode I documented consumption of monarch larvae and destruction of milkweed stems by a dusky-footed wood rat (*Neotoma fuscipes*) (Figure 3.7). I cannot verify this predation event with 100% certainty due to the low resolution of the night vision. However, multiple factors support my identification of the dusky-footed wood rat: (1) What appeared to be a wood rat nest existed in vines and hedges at the edge of the garden, (2) I identified the species by call and physical appearance using a bright headlamp on multiple previous nights in the same location, (3) on multiple nights larvae were present at sunset but absent the next morning with milkweed plants also showing wood rat damage.

Figure 3.6: A scrub jay (*Aphelocoma californica*) consumes a fifth instar monarch larva. A motion detecting camera facing a fifth instar monarch larva on a *Asclepias fascicularis* plant captures the approach, attack, and consumption of the larva by the jay on September 29, 2023.

Figure 3.7: A dusky-footed wood rat (*Neotoma fuscipes*) visits milkweed plants during the night, appearing to consume larvae on multiple nights and removing milkweed branches leaving distinctive cuts on stems. Night vision photos extracted as still images from video taken on September 25, 2023.

Additional predator observations from 2021 through 2024

All other observed predation events were caused by invertebrates. Although I did not witness the capture of the larvae, I recorded a yellow sac spider (presumptive identification *Cheiracanthium inclusum* or *Cheiracanthium mildei*) consuming a monarch larva (Figure 3.8). I also documented Argentine ants (*Linepithema humile*) swarming monarch larvae that had been attacked by *Polistes dominula* (Figure 3.9) and swarming a 5th instar larvae pupating. I also observed an individual *Linepithema humile* ant approaching a 2nd instar larva eliciting a thrashing response by the larva. I observed deceased monarch neonates in the apex of milkweed plants adjacent to small unidentified spiders also in the apex of the plants. I frequently observed individual yellow-jackets (*Vespula pensylvanica*) approach and "buzz" larvae but this did not usually result in a full attack or in larvae dropping from plants.

Figure 3.8: A yellow sac spider (presumptive identification *Cheiracanthium inclusum* or *Cheiracanthium mildei*) consuming a monarch larva. Photo taken by author on July 17, 2021, in residential garden in Berkeley, California.

Figure 3.9: Argentine ants (*Linepithema humile*) swarming monarch larva after larva was killed by a *P. dominula* wasp. Photo taken on August 27, 2021.

As reported in some other studies, many predators would need to initially locate larvae and then would return to consume more (McGruddy 2021; McGruddy *et al.* 2021). Larger fifth instars would usually thrash their heads, followed by dropping from the plant and hiding in near-by ground cover, leading to survival. Argentine ants were common throughout the system. In one garden, Argentine ants would often swarm a monarch corpse after a *P. dominula* wasp had left the site with a prey ball. After returning, the wasp would sometimes move to preen or even carry the ball to a temporary site, preen, and then continue to its nest.

Factors influencing *Polistes dominula* predation on monarch larvae

Temperature

Attacks generally occurred on very hot days and the attacks on hot days were usually fatal (Figure 3.10). Activity of *Polistes dominula* was high on hot days. By late fall, hot days with unseasonably high temperatures such as October 18, 2023, had high activity, but no attacks on larvae. Activity seemed to have switched to wasps searching for nectar or searching for overwintering locations.

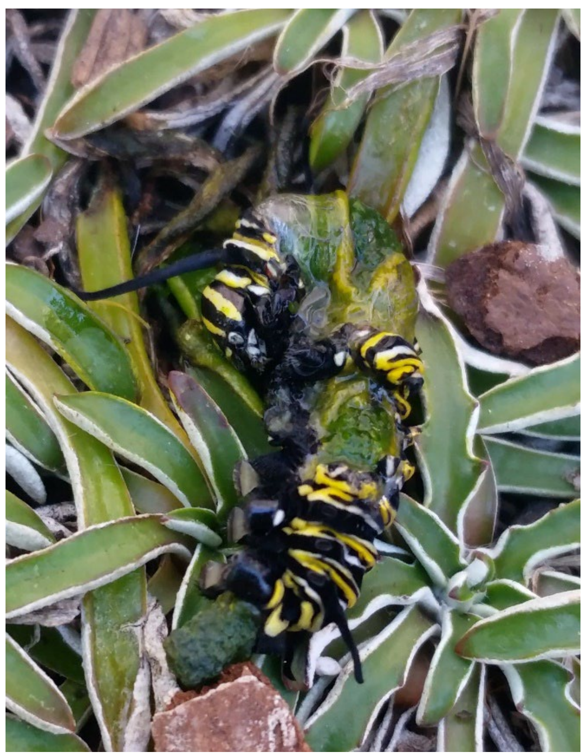

Figure 3.10: An example of a typical fatal attack on a monarch larva by *Polistes dominula*. Larva is partially skinned and still alive after being attacked by a wasp. Photo taken on September 8, 2021.

Plant communities and alternative food sources

Attacks in the Oxford Tract area tended to occur on hot days in the very end of August or in early September. The species of butterflies usually found in urban areas tend to peak in abundance in early fall (Shapiro & Manolis 2007). I suspect that *P. dominula* individuals forage on caterpillars on brassicas and weedy malvas and other easier or more palatable prey and then move on to monarchs once those resources are used. *P. dominula* individuals would travel up and down rows of kale inspecting each plant and orienting themselves by flying up along the fence posts. *P. dominula* do not recruit nestmates and it appears that one individual is usually responsible for all fatalities during a trial. Dense ground cover plants and other debris made it more difficult for wasps to re-locate larvae after they dropped from plants. Larvae escaping to these areas would sometimes survive (Figure 3.11).

Figure 3.11: Monarch larva in the shade after dropping from the experimental plant and escaping into mulching while three *P. dominula* wasps surround the remnants of another larva. It was extremely rare to have more than one wasp involved in an attack. This attack occurred on a hot day after irrigation had been decreased and alternate resources for wasps may have decreased as lepidoptera supporting vegetation decreased. All five larvae in this trial were eventually killed by the *P. dominula* wasps. Photo taken on August 30, 2023.

DISCUSSION

Summary

I divided my study into two parts. In the first part, I sought to identify the primary predators impacting monarch butterfly larvae in urban gardens of the East Bay. After identifying common predators of monarch larvae in the system and determining the predators responsible for the most larval fatalities, I sought to better understand the factors influencing predation pressure and success of these predator species. In the second part of my study, I investigated the factors influencing predation pressure and success of the invasive European paper wasp *Polistes dominula*.

Part 1: Identification of predators of monarch larvae in urban gardens of the East Bay

My central research question for Part 1 of Chapter 3 was: What are the primary predators of monarch butterfly larvae in urban gardens of the East Bay? I found that almost all documented monarch fatalities were caused by invasive *Polistes dominula* wasps.

During extended day and nighttime observations, I observed two species of vertebrate predators consuming monarch larvae: a scrub jay (*Aphelocoma californica*) and a dusky-footed wood rat (*Neotoma fuscipes*). Additionally, I recorded a yellow sac spider (presumptive identification *Cheiracanthium inclusum* or *Cheiracanthium mildei*) consuming a monarch larva. I also documented Argentine ants (*Linepithema humile*) swarming monarch larvae that had been attacked by *Polistes dominula* and swarming a fifth instar larvae pupating. I also observed an individual *Linepithema humile* ant approaching a second instar larva eliciting a thrashing response by the larva. On one occasion, I observed a larval fatality caused by a single *Vespula pensylvanica*.

I had predicted that predators would be diverse, but that the primary invertebrate predators would be both native and non-native wasps. I also predicted that *Polistes dominula* would be the primary invertebrate predator of larger monarch larvae. I also expected that invasive rats and some birds would consume larger monarch larvae and pupae and that ants and spiders would prey upon younger larvae. I had also predicted that *Polistes dominula*, would be an extremely effective larval predator with almost all attacks leading to fatalities. During predator attacks, I expected that monarch larvae would respond to attacks by thrashing their heads, dropping by silk, or rolling into balls and dropping to lower leaves or the ground. Additionally, I expected that monarch larvae on structurally complex plants would be less likely to be preyed upon. I also expected that larvae close to the ground with ground cover or weedy vegetation around a milkweed plant would be able to escape predation by dropping and retreating into the vegetation.

In addition to predators documented by photographs, video, in person observations, and predator physical collection after fatal attacks, I found that predators could often be surmised by patterns in damage to the host plant along with any remnants of the predated larva at the site after the predator had departed. Attacks by birds would often result in broken or heavily bent branches on the upper portions of a plant, large chunks of leaves missing that did not match the normal herbivore damage patterns of larvae, and occasionally a dark green fluid on the leaves near such plant damage. Mammals would often cause severe structural damage to the milkweed plant, severing larger branches and even main stems with sharp diagonal cuts leaving a clean edge. These cuts resembled cuts that could be made by an extremely well-sharpened pair of garden shears, despite the plants not being pruned. Video evidence documented that this damage was caused by a dusky-footed wood rat *Neotoma fuscipes*. To my knowledge, this is the first formally recorded observation of this species consuming monarch larvae.

Some mammals would also shred the milkweed stem into small pieces (Figure 3.12). It was unclear if this was in an effort to consume the plant or an effort to consume any monarch eggs or larvae. This damage was common, especially in early spring, on multiple species of milkweed including *Asclepias curassavica*, *Asclepias fascicularis*, *Asclepias speciosa*, and *Gomphocarpus physocarpus.* I do not recall seeing this damage pattern on *Asclepias linaria*. This could be because *A. linaria* was not a first choice for adult monarch oviposition. I rarely found eggs on *A. linaria* and when I did the eggs were often on new tender leaves and after nearby plants of other milkweed species already had high densities of eggs (personal observations, unpublished regular egg counts in garden of author). Lack of mammalian damage of *A. linaria* plants could also be related to the typically higher concentrations of cardenolides in *A. linaria*, although this did not seem to curtail the damage *of A. curassavica*. Past predation by *Polistes dominula* often resulted in larvae guts and head capsules being discarded near the base of the plant.

Figure 3.12: Shredded stems of *Asclepias*. Photos taken on April 23, 2023.

Part 2: Factors influencing predation pressure and fatality of attacks of *Polistes dominula* wasps on monarch larvae

My central research question for Part 2 of Chapter 3 was: Which factors influence predation pressure and success of the invasive wasp *Polistes dominula*? My sub-questions for Part 2 were: How do temperature and periods of extended high temperatures impact predation by *Polistes dominula*? Can higher than average daily temperatures or multi-day heat waves predict the number of *Polistes dominula* attacks or the fatality of those attacks? And: How does the local plant and insect community in a garden impact predation by *Polistes dominula* on monarch larvae? I found that most fatal attacks occurred on unseasonably hot days in the late summer and early fall with wasps mounting more aggressive attacks on these hot days. I also noted that, during trials in the earlier parts of the summer, attacks were not common in gardens with potentially abundant food resources. Gardens with food crops in the Brassicaceae and other plants potentially supporting insect prey often had no attacks by *Polistes dominula* despite the wasps being abundant in those gardens and displaying hunting behavior. Detailed analysis of this data is still pending.

After observations and predation trials in Part 1, I predicted that predation pressure and attack fatality rates of monarch larvae by *Polistes dominula* would be high, but would vary due to season, temperatures, and the presence of host plants potentially supporting more palatable species of Lepidoptera larvae. Specifically, I had predicted that high temperatures and periods of extended heat would increase the predation pressure and likelihood of fatal attacks. Based on the published reproductive physiology and temperature responses of *Polistes dominula* (Käfer *et al.* 2015; Kovac *et al.* 2022; Liebert *et al.* 2006; Weiner *et al.* 2011), I postulated that increased temperatures would decrease the developmental time of *Polistes dominula* larvae, requiring adults, which are progressive provisioners, to increase their predation rate.

I had also predicted that gardens with abundant insect food sources, particularly lepidopteran larvae, would have lower monarch predation as wasps could choose to select more palatable prey. As more palatable prey are consumed and become a less consistent resource, wasps would increasingly attack less palatable prey such as monarch larvae. Wasps with fewer resources would mount more aggressive and prolonged attacks of larger monarch larvae and would be less likely to be deterred by defensive strategies of larvae, resulting in attacks becoming more fatal.

As a system, I postulated that a combination of high predation pressure by wasps in the mid to late summer combined with seasonal growth patterns of non-native milkweeds *Asclepias curassavica* and *Gomphocarpus physocarpus* might favor monarchs that breed slightly earlier in the spring and much later in the fall and winter. However, the monarchs breeding and feeding on *Asclepias curassavica* and *Gomphocarpus physocarpus* in the fall and winter might encounter higher levels of *OE* spores as leaves remain on summer plants due to high rates of larval predation and resulting low levels of larval herbivory. I expect that pruning non-native milkweeds in the late summer when larvae are not surviving to consume leaves might purge a buildup of *OE* spores from adult visitation on vegetation, potentially resulting in a lower *OE* risk for fall larvae that escape predation once wasp colonies die back and foundresses focus on overwintering. Understanding local patterns could allow gardeners to strategically manage plants using annual environmental cues.

General foraging observations of P. dominula

In my many hours of field observation, I would often observe individual *P. dominula* wasps systematically traversing a garden with little or no interest in floral resources. The majority of my observations were of the wasps carefully hovering between each leaf and branch on selected plants. These observations are consistent with previous studies noting that *Polistes* wasps would search for prey by hovering or walking on plants (Rayor 2004) and that this behavior was common in other social wasps (Ravert Richter & Jeanne 1991). Most of these plants had one or all of the following: (1) visible herbivore damage with holes throughout the leaves, (2) visible frass, (3) were plants that had previously had caterpillars on them, (4) were plant species that were often targeted by lepidopteran larvae in the garden.

In some gardens with drip irrigation, *P. dominula* wasps would follow the irrigation lines but it was unclear if they were searching for water or prey. In the SOGA garden, these irrigation lines were often surrounded by weedy plant species. Many of those weedy plant species are larval host plants for some of the more common urban butterflies that I observed in the study gardens. Urban butterfly species are often described as "weedy" and utilize the primarily non-native plants and weeds present in the human constructed and regulated landscape (Shapiro & Manolis 2007). These plants are often dependent in part on human regulated irrigation systems.

Predation patterns and seasonality of other Lepidoptera

Predation patterns are likely influenced by the unique species and seasonality of urban butterflies in the system. As previously described, the Mediterranean climate of the San Francisco Bay area experiences late summer and early fall temperatures that are very different from those in much of the United States. The highest temperatures are generally August and September with hot days extending well into October. The highest annual butterfly densities in these systems occur in September and October in the Bay Area. Further inland, butterfly populations peak in early October and few butterflies are seen in gardens before late July (Shapiro & Manolis 2007). Depending on larval and pupal predation, the highest density of corresponding butterfly species larvae is likely in the weeks before these peaks.

Larger butterfly community and options in palatability

I also observed that individuals of *P. dominula* would spend large amounts of time inspecting a grove of variegated geranium (*Pelargonium* spp.) that had frass, physical damage, and frequent larvae. A larger instar was knocked off of the plant by an individual of *P. dominula*, but the wasp did not pursue the larva once it had dropped to the ground. I subsequently reared this larva on cuttings of the same plant and my identification of the resulting adult moth species is pending.

Reproductive biology and overwintering practices of Polistes dominula

Scientists have suggested that the rapid spread of *Polistes dominula* in the United States could be the result of an ability to rapidly colonize new structures combined with a generalist diet and a mismatch in breeding times and times of high predation by birds and other wasp larvae predators (Cervo *et al.* 2000; Liebert *et al.* 2006). In their native environments in southern and central Europe, *Polistes dominula* rapidly colonize newly available structures and become increasingly dominant with time (Cervo *et al.* 2000; Liebert *et al.* 2006). *Polistes dominula* may allow for high nest density and reuse of nests from previous years by overwintering foundresses and early season breeding in locations with high prey availability.

For example, one study garden had a high density of *Polistes dominula* adults year to year. While I did not directly observe any larval monarch fatalities caused by the species, the garden had very few to no larvae present during times of high *P. dominula* predation in nearby gardens. I also observed numerous non-fatal attacks on monarch larvae by *P. dominula* during predation trials in that garden. After searching for nests under awnings, roofs, and other potential nesting structures on the property and adjacent lots with the permission and assistance of property owners, I located a large nest of *P. dominula* in a cable box and utility pole in the garden's green strip on an unseasonably hot fall day (Figure 3.12). While monarch larvae were not attacked or killed during that day's trial, wasp activity was high. I was able to locate an extensive comb network inside a cable box that was not properly sealed. While little to no activity was visible at the nest most days, activity was high on all hot days including the observation date of October 7, 2023. Given the amount of nesting locations in the utility pole and cable box, I suspect that many foundresses overwintered in the structures and that predation on larval monarchs was influenced directly by those wasp colonies. Property owners had previously petitioned the regional power company Pacific Gas and Electric (PG&E) to replace the dilapidated utility pole for multiple years with PG&E taking no action. Given that property owners did not have ownership of the pole or cable box, property owners and the surrounding neighborhood were left with little recourse.

Figure 3.13: A dilapidated utility pole and cable box containing large numbers of *Polistes dominula* wasps. Photo taken on October 7, 2023.

Limitations and future directions

Limitations

My 2023 predation trials were primarily limited to one species of milkweed and to trials from August through early October of 2023. The California state Department of Fish and Wildlife heavily regulates all activities involving monarch butterflies including research activities and activities occurring outside of conservation lands and on private property. It was not possible to purchase monarch eggs from a commercial supplier nor to establish a research breeding colony to source eggs. All experimental larvae were reared from eggs that had been oviposited by free-ranging monarchs on designated "egg collection" plants in a small private residential urban garden (CDFW SCP S-230290001-23074-001). These restrictions influenced the timing of experiments, particularly during the early summer of 2023, as predation trials could not be conducted if eggs did not exist. Because oviposition by adult monarchs during May and June was extremely limited, I could not obtain eggs and, consequently, could not obtain larvae for early summer predation trials. Despite this restriction, I was able to observe predation events when they did occur. Wasp activity and predation of larvae was consistently low during early summer and was concentrated in the late summer and early fall.

After mid-October, predation on monarch larvae drops and most larvae can be observed day to day on the same plant, presumably because they are not being consumed. From mid-October until the early summer, insect predators do not appear to cause many larval monarch fatalities. I suspect that the primary predators in late fall through the winter are birds and small mammals. During fall, many birds will forage, apparently for seeds, in larger shrubs and I suspect that they consume any larvae or pupae that they encounter. Pupae in such shrubs would often disappear without a trace during daytime hours overlapping with high foraging activity of these small birds. As shown in Figure 3.6, predation by birds can occur within one or two seconds, leaving little evidence beyond broken or bent branches.

Future directions

Future directions should focus on early monitoring and management of *P. dominula*. The range of *Polistes dominula* is likely to continue to expand including to regions with other monarch populations (Howse *et al.* 2020). While fermented fruit lures have been used to trap other species of *Polistes*, these traps are not effective for *P. dominula* (Landolt *et al.* 2014). *Polistes*-specific traps are rare in gardens in the region. Most gardeners, including those who are very knowledgeable about insects, utilize yellow jacket traps only (personal observations). The most commonly available commercial trap in the region for *Polistes* uses three lures (2-methyl-1-butanol, heptyl butyrate, and acetic acid) to target multiple species including *Polistes*. However, after setting these traps in two of the study gardens with high numbers *of P. dominula* sightings, I did not capture any *P. dominula* adults or any other *Polistes* species over multiple years. One of the two locations was adjacent to a utility pole and cable box containing one or multiple large colonies. The *Polistes* portion of this trap relies on a tube of attractant that must be replaced regularly along with water and dish soap added to the container. It can be challenging to set up and replace the *Polistes* attractant tube due to the presence of live captured yellow jackets in the bottom compartment. Homemade traps created by colleagues for their own gardens also failed to trap *P. dominula* (personal communication with Kipling Will). Additionally, if traps are not catching *Polistes dominula*, *Polistes*-specific traps may attract and kill native *Polistes* that are not posing a threat to monarch larvae in gardens. Future directions should also include more observations of nocturnal predators, which have not been frequently documented in the literature (Myers *et al.* 2020).

Broader implications

Given that traps are not currently working in the system, public education could help to address the threat of *P. dominula* wasps to monarch larvae. Outreach campaigns could focus on teaching gardeners how to locate *P. dominula* nests early each season, preventing colonies from growing in size throughout the summer. Outreach could also help property owners better secure structures to prevent large colonies from forming in difficult to access and hidden nesting locations. Utility companies such as PG&E could replace dilapidated utility poles and cable companies could fully close and seal cable boxes, decreasing the chances of wasps using such difficult to access locations for nesting.

Outreach could also help property owners distinguish between species of wasps that may look similar to the untrained eye. A large yellow and black mud-dauber (*Sceliphron caementarium*) may appear threatening to a gardener and may appear similar to *P. dominula* from a distance. A spider-specialist blue mud wasp (*Chalybion californicum*) or a large Pompilid wasp may appear to be a threat and gardeners may be tempted to remove old mud nests from houses or trample locations with underground solitary wasp nests. However, they would be missing out on enjoying these lovely native animals that pose no threat to their monarchs. Understanding local larval monarch predation can help to protect other species of invertebrates through better understanding of urban insect diversity.

There is something uniquely horrifying about losing a beloved caterpillar. Gardeners purchase, grow, and maintain larval host plants simply for the chance of an adult butterfly leaving a tiny egg to grow into a plump caterpillar. As many gardeners check for new blooms at the start of each morning, caterpillar enthusiasts often search their plants for eggs. Each successive instar brings new excitement. But sometimes, we go to check on our caterpillars only to find a partially skinned wriggling larva being dismembered by a wasp. This is not an enjoyable moment. Other predation events are less brutal – the larvae simply disappear. In that disappearance gardeners lose a piece of daily joy and countless hours of hard work. Low-cost camera setups, such as the ones used during my extended day and nighttime observations, could help gardeners to understand the fates of their disappearing larvae. We want to know what gobbled up our caterpillars.

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