

Commentary

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Western North American Monarchs: Spiraling into Oblivion or Adapting to a Changing Environment?

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Abstract: Monarch butterflies in western North America typically migrate each fall from the Pacific Northwest to overwintering sites in California. Winter 2020/21 saw the lowest number of overwintering western monarch butterflies ever recorded, but was also marked by a winter-breeding population in the San Francisco bay area that appeared to be the largest ever seen. Recoveries of monarchs with wing tags from the Pacific Northwest suggested that many non-reproductive migrants in fall 2020 became reproductive in the San Francisco bay area and did not reach coastal overwintering sites. Mean daily maximum temperatures for San Francisco during fall and winter increased by ~1 °C during the past decade and were 2.5 °C above the 30 year mean during September–October 2020. Warm fall and winter temperatures along with the availability of non-native milkweeds likely caused the increase in winter breeding in winter 2020/21. The outcome of continued winter-breeding in the San Francisco bay area is uncertain. Whether it becomes a sink or source will be dependent on whether winter-breeding monarchs can re-enter their migratory state during spring. However, endemic levels of infection by the protozoan parasite, *Ophryocystis elektroscirra* (OE), are often high in winter-breeding monarchs which can limit migration success. The eventual co-existence of winter-breeding

and non-breeding monarch populations in northern and central California is probable, with an optimistic view suggesting that the adaptability of the monarch butterfly will allow it to persist in a changed environment.

Keywords: Migration, Overwintering, Winter-breeding, Non-native milkweeds, Climate warming, *Ophryocystis elektroscirra*

The monarch butterfly, *Danaus plexippus*, in North America is famous for its annual fall migration from breeding areas to selected overwintering sites, where they cluster on trees and await the return of spring. The population is roughly divided by the Rocky Mountains, although recent genetic evidence suggests there is considerable gene flow between individuals east and west of the mountains [1]. The western US population has always been smaller and has received less attention than the much-vaunted eastern US population [2]. However, the migration of western monarchs is just as remarkable as the migration of eastern monarchs, transferring populations from west of the Rocky Mountains to overwintering areas along the California coast followed by a return migration in spring [3, 4]. Historically, hundreds of overwintering sites along the California coast each with thousands of butterflies, have been visited by thousands of sightseers, and on a small scale, mirrored the spectacle of millions of overwintering monarchs in Mexico.

The numbers of monarchs that cluster at these overwintering sites has been tallied over time and on January 19 2021, our worst fears for western monarch butterflies came to fruition. The numbers for the 2020 Thanksgiving count showed that the western monarch population had hit rock bottom. Just 1,914 butterflies were found at 246 overwintering sites in coastal California, an average of 7.8 butterflies per site. Contrast that to 1997, the year counts started, when an average 12,233 butterflies were found at each of 101 sites for a total of > 1.2 million butterflies (<https://www.westernmonarchcount.org/>). This suggests a 98-99% decline in the western monarch population during the past 23 years. Unsurprisingly, there has been

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much talk of ‘extinction’ of this population in news media and online forums (<https://xerces.org/blog/western-monarch-population-closer-to-extinction-as-wait-continues-for-monarchs-protection>), particularly in light of the decision to preclude monarch butterflies (as a species) from federal protection for now (<https://www.fws.gov/savethemonarch/ssa.html>).

However, something else appeared to be happening with monarchs in California this winter. There was an unprecedented increase in monarch breeding activity, particularly around Los Angeles and San Francisco. Unfortunately, much of the evidence for this is anecdotal and/or reported in social media forums, but it does appear to be real. In a recently submitted manuscript (accessible as a pre-print) Crone and Schultz [5] estimated 12,000 monarchs were resident in summer 2020 in near-coast urban gardens in northern and central California, an estimate extrapolated from densities in Berkeley, CA gardens.

A simple analysis of monarch larvae and pupae records in the San Francisco Bay area contributed to the iNaturalist web site (<http://www.iNaturalist.org>) during each January from 2015 to 2021, provides a startling snapshot of what may be happening (Fig. 1). The San Francisco bay area which prior to 2020, hosted only a few records of monarch larvae and pupae each January, provided 60 records in January 2021. Most of these larvae and pupae were associated with non-native milkweeds, the monarch host-plant (*Asclepias curassavica*, *Gomphocarpus physocarpus*, *Gomphocarpus fruticosus*). A similarly dramatic increase also occurred in the number of monarch adults reported in January 2021 (Fig. 1).

If substantial winter-breeding of monarchs in the bay area is a new reality, there are many important questions

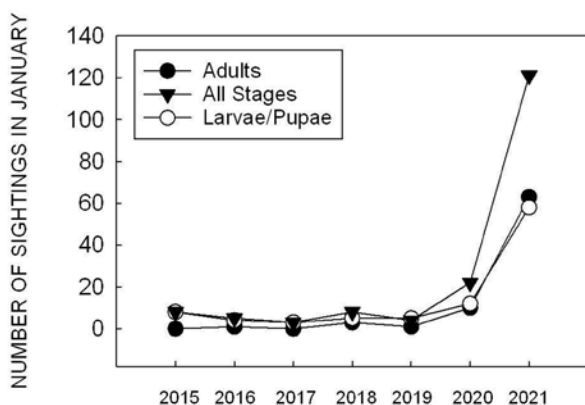


Figure 1: January sightings of monarch larvae/pupae and adults in the bay area of San Francisco reported to <https://www.inaturalist.org/> during 2015-2021. Data extracted February 2021.

that we need answers to, so that we can make decisions about how to best support western monarch populations going forward. Here are four of the most compelling:

1. Is the apparent increase in bay area **winter breeding**, linked to the declining overwintering population in California?
2. Are **non-native ornamental milkweeds** helping to terminate reproductive dormancy and migration in fall migrants?
3. Is the **warming climate** encouraging fall migrants to breed during winter rather than overwinter as non-breeding adults?
4. How will the potentially high levels of the **parasite *Ophryocystis elektroscirra* (OE)** in San Francisco bay area winter-breeding populations affect monarch migration biology?

1 Is the declining non-reproductive migratory population associated with the increasing winter reproductive population?

Historically, most western monarchs migrate during fall from the Pacific Northwest (PNW), inland California, Nevada and Arizona to overwinter in a non-reproductive state at ~300 coastal California sites stretching from Mendocino County in the north to San Diego in the south [3, 4, 6]. In 2017, a single tagged monarch female released in Oregon on September 3 flew 877 km in 19 days and was photographed ovipositing on young *A. curassavica* plants in Santa Barbara, CA [7]. This was the first evidence that a fall migrant from the PNW could become reproductive at its California destination and likely not join an overwintering colony. A second instance occurred in 2019, when a tagged female from Oregon flew 537 km in 40 days and was photographed ovipositing on *A. curassavica* in Palo Alto on October 24 in the bay area of San Francisco [4]. Are these two reports, just the tip of the iceberg? How many other fall migrants become reproductive when they reach the San Francisco and Los Angeles urban areas and places in between? After two years (2018, 2019) with counts of 27,000-29,000 overwintering butterflies at CA overwintering sites, the drop in 2020 to 1,914 was precipitous. It is possible that in 2020 there were at least as many, or more fall migrants, that formed winter-breeding populations in California, in addition, perhaps to the estimated 12,000

butterflies already present in near-coastal urban areas in northern and central California [5].

Further evidence for an increased number of fall migrants joining reproductive populations in the San Francisco bay area in 2020 comes from our PNW tagging program [3, 4]. Since 2012, citizen scientists in the PNW in association with Washington State University have reared and tagged monarchs with the majority of recoveries (63%) made at overwintering sites in California. In 2020, 1300 monarchs were tagged in late summer and fall but zero were found at overwintering sites for the first time. Since 2014, our overall annual average recovery rate for tagged monarchs was 0.66%. In 2020, this recovery rate was 0.77%. Thus, we recovered as many tagged monarchs in 2020 as expected. The difference was that all of them were found during migration instead of at overwintering sites. The number of tagged monarchs we recovered during the fall migration in 2020 was eight times greater than the average for the previous six years. All tag recoveries in 2020 were made of live monarchs, photographed and reported by email, in inland N CA and in the San Francisco bay area (Fig. 2). Unlike other years, tagged monarchs in 2020 did not appear to move coastward to towns like Santa Cruz and Pacific Grove that host overwintering sites. This may have been representative of general non-arrival at overwintering sites by fall-migrating monarchs in 2020.

Our data on tagged fall migrant monarch recoveries in N CA and the San Francisco bay area along with data on winter observations of larvae and pupae in the bay



Figure 2. Male monarch tagged in Brookings, Oregon on October 11 2020, pictured feeding from *A. curassavica* flowers at Benicia in the San Francisco bay area on October 24 (Photo: Teresa Chang).

area during winter 2020/21, presents a signal, of a possible changing dynamic in monarch butterfly migration and overwintering ecology in the western US. Among the many reports of monarch activity and breeding during winter 2020/21 were indications that sizeable breeding populations existed in some urban habitats like community gardens and business landscapes. Almost 100 individual sightings of monarch life stages in a small area of Santa Clara county were made during November 2020-February 2021. Sightings of 30 or more adults counted during 30-minute survey walks in January-February 2021 were also reported at a site in Santa Clara county as were reports at another site in the same county of significant egg-dumping on bare stalks of *G. physocarpus* and *A. fruticosus* (Fig. 3) (K. Krimmer and M. Schaefer, pers. comm.). Counts of 100-200 eggs on a dozen or so plants, were also reported. A visit to these two Santa Clara county sites in late February 2021 by the author, produced estimates of ~100 adults and counts of 150 eggs and a dozen late instar larvae in four hours of walking and observation (DGJ unpubl. obs.) These observations suggest the presence of large winter-breeding populations in some locations in the San Francisco bay area.

The evidence to date, suggests that there is a link between declining populations of monarchs at traditional coastal overwintering sites, and the emergence of substantial winter-breeding populations in the San Francisco bay area. However, further work is needed to confirm this.



Figure 3. Monarch eggs ‘dumped’ by females in January 2021 in Palo Alto, Santa Clara County, CA on a cut and leaf-bare stalk of *G. physocarpus* (Photo: Karen Krimmer).

2 Are non-native Milkweeds helping to cause premature termination of migration and reproductive dormancy in monarchs?

Most of the observations on larvae and pupae in the Bay area reported during winter 2020/21 to iNaturalist, social media sites and to me, were associated with two non-native milkweed host plants (*A. curassavica* and *G. physocarpus*). However, there were some instances in November and December 2020 of larvae associated with still-green native milkweeds, *Asclepias speciosa* and *Asclepias fascicularis*. Some studies have suggested a link between non-native milkweeds and termination of migration in eastern US monarchs [8, 9]. Clearly this association will be of concern if non-native milkweeds help terminate the migration and reproductive dormancy of fall migrants in the western US. However, evidence from Australian monarchs shows that winter reproductive dormancy is maintained at overwintering sites despite the presence of the African milkweeds *G. fruticosus* and *G. physocarpus* [10, 11]. Furthermore, the presence of milkweed at overwintering sites appears to be a pre-requisite for establishment and maintenance of overwintering, non-reproductive monarch populations in Australia [11]. While migrating and non-reproductive monarchs may have evolved since their arrival in Australia in the late 1800s to be non-responsive to milkweed at overwintering sites, this may not be the case for migratory eastern US monarchs, which have been shown to respond to the presence of non-native milkweed by becoming reproductive [9]. Western US migrating monarchs may also respond to non-native milkweeds by breaking reproductive dormancy and terminating migration, but research is needed to confirm this. It is becoming increasingly evident that despite being identical genetically, western and eastern monarchs can and do differ behaviorally and physiologically [1], and we cannot assume that what applies to eastern monarchs, applies to the western population as well [4].

3 Is a warming climate causing more fall migrants to become reproductive in the San Francisco Bay area?

There is little doubt that the climate in California is warming with some estimates suggesting an increase of $> 0.5^{\circ}\text{C}$ per decade over the past 30 years (<https://monarch-watch.org/blog/2020/02/25/monarchs-and-climate-in-the-west/>). In the 1960s, winter breeding of monarchs in California was confined to an area south of San Diego [12]. Since then, winter breeding has become common in the Los Angeles area [8] and now, the San Francisco bay area. However, this northward expansion of winter-breeding may have been facilitated as much by increased availability of non-native milkweed host plants in urban areas, as by warmer conditions.

The 30-year (1985-2015) mean daily maximum temperature for San Francisco during meteorological winter (December-February) is 14.3°C (<http://www.timeanddate.com/weather/>). However, data extracted from this web site for winters since 2013/14 indicate the mean daily maximum temperature for San Francisco has increased to 15.1°C (Fig. 4). If a warming climate is encouraging migrants to become reproductive in the bay area, this should happen during September-October, the period when maximum numbers of migrants fly through San Francisco heading for coastal overwintering sites [3, 4].

The web site, <https://www.timeanddate.com/weather/>, shows the 30-year (1985-2015) mean daily maximum temperature for San Francisco during Septem-

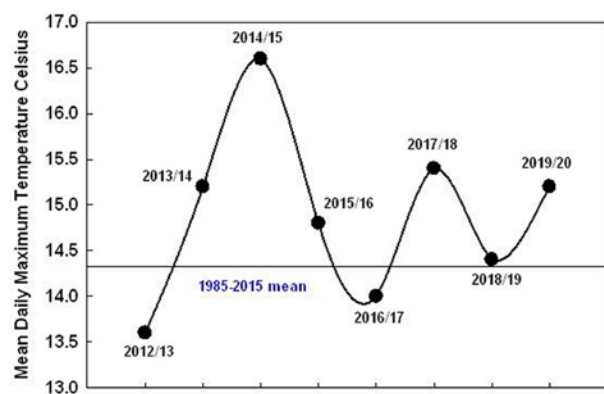


Figure 4. San Francisco mean daily maximum temperatures ($^{\circ}\text{C}$) for winter (December-February) from 2012/13 to 2019/20, compared to a 30 year (1985-2015) mean. Data from <https://www.timeanddate.com/weather/>

ber-October to be 22.2° C. Data extracted from this site for 2014-20 show that this has increased to 23.3° C (Fig. 5). The mean daily maximum temperature for September-October 2020 was 24.7° C, 2.5° C above the historical mean. Migrants in the bay area in September 2020 were frequently exposed to warm temperatures in the 30s up to 39° C.

The nature of reproductive dormancy and associated migratory behavior has not been characterized in western US monarchs. They have been at least partially characterized in Australian and eastern US monarchs [10, 13]. While reproductive dormancy in eastern US monarchs is characterized as reproductive diapause [14] (defined by a prolonged physiological refractory phase when butterflies cannot respond normally to stimuli like temperature, photoperiod and host plants), the many reports of butterflies becoming reproductive in southern states during fall [15], indicate that diapause is not characteristic of the entire population. Reproductive dormancy in Australian monarchs is essentially physiologically flexible, maintained behaviorally, and known as oligopause [16, 17, 18]. This type of reproductive dormancy can be broken at any time by exposure to warm temperatures and long daylengths. Reproductive dormancy in western US monarchs may also have a high degree of plasticity.

Historically, reproductive dormancy has been sustained during migration through the bay area in September-October with scant evidence of winter breeding prior to 2020/21 (e.g. Fig. 1). The mean daily maximum temperature of 24.7° C in September-October 2020 may have terminated reproductive dormancy and migration in a sizeable proportion of the migratory population, thus creating a large winter breeding population in the bay area.

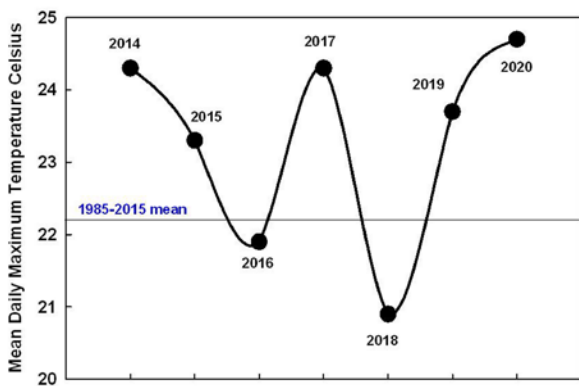


Figure 5. San Francisco mean daily maximum temperatures (°C) during September-October from 2014-2020, compared to a 30 year (1985-2015) mean. Data from <https://www.timeanddate.com/weather/>

It seems likely that the warming fall and winter climate evident during recent years in the San Francisco bay area, has promoted the increase in winter-breeding populations in this region, facilitated by the increased presence of non-native milkweeds.

4 Will high levels of the parasite *Ophryocystis elektroscirrha* (OE) in San Francisco bay area winter-breeding monarchs affect migration biology?

It seems likely that winter-breeding of monarchs in the San Francisco bay area and Los Angeles basin is largely supported by home garden and commercial cultivation of *A. curassavica* and other non-native milkweeds. Monarchs breeding during winter in southern California on *A. curassavica* were shown to harbor increased levels of the protozoan parasite *Ophryocystis elektroscirrha* (OE) [8]. This parasite, at high levels, is known to degrade the fitness of eastern US monarchs [19, 20]. If winter-breeding monarchs in the San Francisco bay area are able to migrate northward in spring, will this behavior be badly compromised by widespread and high levels of OE infection as suggested by Crone and Schultz [5]? While Satterfield et al [8] showed high levels of OE were prevalent in winter breeding monarchs in the Los Angeles area, this may not be the case in the cooler-climate San Francisco bay area. Non-native milkweeds are readily available from California nurseries and stores and have seen a surge in popularity in recent years. This is despite warnings from conservation organizations that non-native milkweeds exacerbate monarch OE infections and spread (<https://monarchjointventure.org/blog/qa-about-research-related-to-tropical-milkweed-and-monarch-parasites>). It is recommended that *A. curassavica* plants in California be cut down to ground level in October or November to break the OE life cycle and this guideline is often followed. At two Santa Clara County breeding sites studied during winter 2020/21, one had a mixture of pruned and unpruned non-native milkweeds (*A. curassavica*, *G. physocarpus*) and smaller numbers of a native milkweed (*A. speciosa*). The second site had the same milkweeds, but most of the non-native plants were pruned in October with the reported loss of monarch eggs and larvae. The pruned milkweed stalks continued attracting female monarchs during the winter which laid large quantities of eggs on

them (Fig. 3) resulting in caterpillars that mostly starved. Clearly, this presents a dilemma. Should we continue pruning non-native milkweeds, imperfectly preventing breeding, or should we allow these milkweeds to support monarch larvae during winter that may carry high levels of OE? Allowing non-native milkweeds to grow during winter will likely increase OE levels in breeding monarch populations. However, if winter breeding monarchs in San Francisco ultimately become migratory in spring, this may help ‘cleanse’ the population of OE, as suggested occurs with the fall migration in the eastern US [8], although this would require most of the population to migrate in spring. Recent limited data suggested that western monarchs infected with OE are still able to migrate from the PNW to California and overwinter [4]. While far from conclusive, these data highlight the necessity of investigating OE impacts on western monarch populations and not extrapolating from research on eastern populations.

The impact of OE on the functionality of winter-breeding populations of monarchs in the San Francisco bay area, will depend on the levels of infection and extent of infection within these populations. OE will reduce the success of winter-breeding, but whether this reduction will prevent functionality including migration is unknown.

5 Concluding Remarks

Will winter breeding be successful in the San Francisco bay area? Killing frosts are now relatively rare in this largely urban region and although winter development of eggs, larvae and pupae is slow, it is likely that adults will be produced. Large numbers of newly-eclosed adults were reported during January-February 2021 in Santa Clara County (Karen Krimmer and Maria Schaefer pers. comm.) Slow development will result in prolonged exposure to natural enemies but this may be counter-balanced by reduced populations of predators and parasitoids during the winter months. A peak in numbers of freshly-eclosed adults was observed during early January 2021 at two breeding sites in Santa Clara County, and were likely the progeny of fall migrants. A further generation of adults occurred in March.

Whether winter breeding populations in the bay area become a ‘sink’ or a ‘source’, largely depends on whether developing larvae/pupae during March-May respond to the environmental cues of increasing daylength and temperatures to produce migrants, and how severe endemic OE infection levels are. Traditionally, when individuals leaving coastal overwintering sites migrate inland during

February-March, they travel only a few hundred kilometers at most [21]. The next generation of larvae developing in central and northern California during March-May, respond to increasing daylengths and temperature, producing migrants that reach into Oregon. It is possible that there will be no difference between this generation and a San Francisco bay area winter-breeding generation developing during a similar time-frame, in terms of producing migrants. It is unlikely that the winter-breeding population will lose the ‘genetic tendency to migrate’ as suggested by Crone and Schultz [5].

I have been involved with monarchs for 43 years, and the single, overriding thing that I have learnt is that the monarch is a highly adaptable insect! It has an incredible ability to adjust to changing environmental circumstances. In Australia, it took the monarch less than 75 years to change its core physiology as part of adaptation to a different climate [10]. I therefore have a more optimistic view of the outcome of altered winter ecology of monarch butterflies in the west than postulated by Crone and Schultz [5] who state ‘monarch migration is on the brink of disappearing from the west’. From the available evidence, increased winter-breeding population of monarchs in the bay area in 2020/21 is likely to be directly related to the conversion of fall migrants to reproduction induced by warm temperatures in September-October and widespread availability of non-native milkweeds. Consequently, this population may be responsive to environmental cues (increasing daylengths and temperatures) during March-May and provide spring migrants for summer colonization of the interior west and PNW. How many migrants and how fit they may be, especially in terms of OE infection, are however, major uncertainties at this point.

If the San Francisco bay area winter-breeding population does not help repopulate inland CA and the PNW by producing spring migrants, there is still another possible scenario that may help avoid ‘completely losing monarch butterflies from the interior west’ [5]. Lincoln Brower and Robert M Pyle recognized almost 20 years ago that there was a significant annual incursion of eastern monarchs into the west through westward movement of spring migrants from overwintering colonies in Mexico [22]. In some years, this westward spread of eastern monarchs may be substantial and it is likely the cause of many spring sightings in Arizona and Utah. In summer 2020, despite the virtual absence of monarchs in the northern half of Oregon and Washington, good numbers were seen in Utah and Idaho, possibly as a consequence of ‘leakage’ of eastern US monarchs to western states bordering the Rocky Mountains. In a favorable year for incursion, eastern monarchs may have the potential to help repopu-

late a larger area of the western US. Brower and Pyle [22] also suggested that population incursion from the east might be fundamental to the long-term sustainability of the western monarch population.

Consideration of new long-term strategies to conserve and enhance the western monarch population must await evidence on the future nature of migration and winter breeding in California. Will winter-breeding in the San Francisco bay area continue to be a feature of monarch ecology as it is in the Sydney basin of Australia? The overwintering monarch population in Sydney fell by > 90% from the early 1960s to late 1970s [11]. Winter-breeding was not a feature of Sydney populations in the early 1960s [23], yet it was by the late 1970s [24, 10]. Although habitat-loss and degradation were postulated as reasons for the monarch population decline [10, 11], it is possible that conversion of some of the fall migrant population to breeding populations was also a factor. Non-reproductive overwintering populations, albeit at a reduced level, continue to occur in Sydney, alongside breeding populations [11]. It is important to note that both types of population, resident reproductive and migratory non-reproductive continue to exist in Sydney, Australia, although the spectacular overwintering colonies seen in the mid-1960s (colony populations up to 40,000 butterflies), no longer occur. This is potentially a scenario, which may be evolving in California: reduced migratory, non-reproductive overwintering populations and equal or larger-sized winter breeding populations which may be heavily infected with OE. California, similar to the Sydney Basin, may be moving towards hosting annual winter-breeding and non-breeding monarch populations, due to climate warming and facilitated by increased availability of non-native ornamental milkweeds.

Four decades after confirming the existence, and studying the biology of breeding and non-breeding winter monarch populations in Australia, I feel a strong sense of déjà vu. Time will tell, if western US monarch populations are evolving a comparable overwintering ecology in California, but I do know one thing. The high adaptability of monarchs ensures that the monarch butterfly will persist in western North America. The real question is: how will future populations compare to historical populations?

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