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VIEWPOINT

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Resilience or Catastrophe? A possible state change for monarch butterflies in western North America

Elizabeth E. Crone[1] | **Cheryl B. Schultz**[2]

[1]Department of Biology, Tufts University, Medford, MA, USA
[2]School of Biological Sciences, Washington State University, Vancouver, WA, USA

Correspondence
Elizabeth E. Crone, Department of Biology, 200 College Ave, Medford, MA 02155, USA.
Email: elizabeth.crone@tufts.edu

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Abstract

In the western United States, the population of migratory monarch butterflies is on the brink of collapse, having dropped from several million butterflies in the 1980s to ~2000 butterflies in the winter of 2020–2021. At the same time, a resident (non-migratory) monarch butterfly population in urban gardens has been growing in abundance. The new resident population is not sufficient to make up for the loss of the migratory population; there are still orders of magnitude fewer butterflies now than in the recent past. The resident population also probably lacks the demographic capacity to expand its range inland during summer months. Nonetheless, the resident population may have the capacity to persist. This sudden change emphasises the extent to which environmental change can have unexpected consequences, and how quickly these changes can happen. We hope it will provoke discussion about how we define resilience and viability in changing environments.

KEYWORDS
alternative stable states, *Danaus plexippus*, disease ecology, ecological surprises, ecological trap, source–sink dynamics, urban ecology

INTRODUCTION

Ecological dynamics are often surprising (Doak et al., 2008). By now, many ecologists have realised that some unlikely events are likely to happen (Pielke & Conant, 2003), and that systems might suddenly shift between alternate stable states (Beisner et al., 2003). In some cases, rapid declines of species can be attributed to a single stressor, and removal of that stressor leads to rapid recovery (e.g. raptors and the pesticide DDT; Grier, 1982). In others, once-abundant populations cannot recover after steep declines, even after obvious threats are removed (e.g. passenger pigeons, Halliday, 1980). In fisheries, overharvest can lead to alternative stable states, specifically, changes in population structure such that populations cannot recover even after harvest ends (Persson et al., 2007). Nonetheless, the operating paradigm in management of at-risk species is that declines in abundance will occur at a pace for which conservation biologists and managers have time to assess a species' status and make recovery decisions over the course of processes that take years to implement. There is also an implicit assumption that removing the stressor that caused declines will allow a population to recover, which is not always the case.

Here, we explore sudden and dramatic changes in the abundance, distribution and demography of monarch butterflies in the western USA. Rather than waiting for complete understanding, we describe these startling changes as they are occurring. We use simple calculations and available data to put these changes in the context of what we know about the current and likely future status of this population. We hope to inspire discussion about how we define population viability, and how we use ecology to guide management in the face of biological uncertainty.

STATE OF THE MONARCH BUTTERFLIES IN THE WEST

Western monarch butterflies are distinct from the larger, eastern monarch population that overwinters in Mexico and breeds east of the Rocky Mountains (Freedman et al., in press), and they are in greater peril (Espeset et al., 2016; Pelton et al., 2019). Until now, western monarch butterflies bred throughout the western states during the summer (Figure 1a). In fall, these western monarchs would migrate to the California coast and spend the winter clustering in a partly dormant state in groves of pine and eucalyptus trees. In the 20th century, millions of monarch butterflies clustered in these overwintering groves. However, by the 2010s the number of overwintering butterflies in the West had dropped from millions to two or three hundred thousand (Schultz et al., 2017). In 2018 and 2019, this number dropped to about thirty thousand (Pelton et al., 2019). In the fall of 2020, only about two thousand butterflies showed up (Xerces Society, 2021). These declines have been attributed to degradation of wintering groves and summer breeding habitat, expansion of pesticide use and interacting effects of climate warming (Crone et al., 2019; Pelton et al., 2019). Although monarch butterfly migration persists east of the Rocky Mountains, the phenomenon of monarch migration is on the brink of disappearing from the West (Figure 1b).

At the same time, monarch butterflies are abundant in gardens in cities on the California coast. No one has been counting these urban butterflies, but people living in coastal cities say they may be getting more abundant through time. One rough measure of a non-migratory urban population is reports of monarch breeding in summer near the coast, which have increased dramatically in recent years (Figure 1c, Supplemental analysis S1; see also James, 2021). This number is not a perfect estimate of the urban monarch butterfly population – for example, it could mean that more people on the coast have become interested in reporting butterflies – but it is generally consistent with the notion that monarch butterflies are becoming year-round residents in coastal cities, at the same time as the migratory population is disappearing.

CAN NEW RESIDENTS REPLACE OLD MIGRANTS?

One of the most obvious first questions is whether the increase in resident monarch butterflies can replace the decline in the migratory population. To get a more

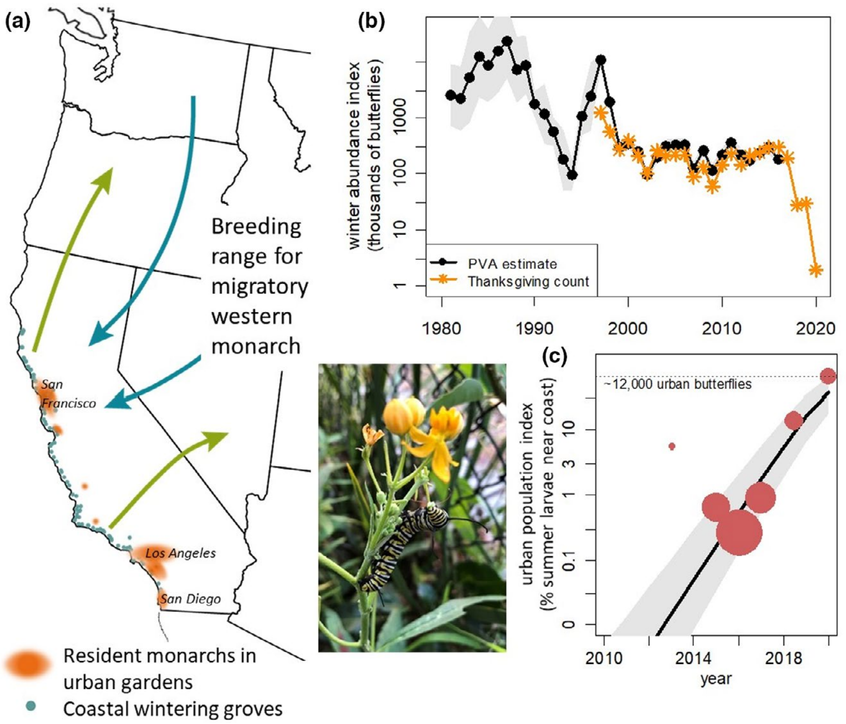

FIGURE 1 Change in status of western monarch butterflies. (a) Breeding, overwintering and resident range of western monarch butterflies in the Western USA. (b) Trends in the migratory population through time, based on historical records and the Western Monarch Thanksgiving Count. The black line shows estimates from a state-space population viability analysis (PVA; Schultz et al., 2017) with 95% confidence intervals. The orange stars are raw counts from the Western Monarch Thanksgiving count, showing the steep decline in recent years. (c) Increase of sightings of immature monarch butterflies (eggs, larvae and pupae) near the coast, as a rough indicator of increasing abundance of a resident urban population of monarch butterflies. Data are from the Western Monarch and Milkweed Occurrence Database (2018). Point area is proportional to the number of sightings during each time period. The black line shows predictions from analyses of year-round breeding, shown for summer months (June–August) because migratory monarch butterflies do not breed in winter, with confidence intervals in grey. The estimate of ~12,000 urban butterflies comes from ground surveys in 2020–2021. See further details in supplement S1 (analyses of sighting records) and S2 (estimating the resident population size). The photo is of a monarch butterfly caterpillar on tropical milkweed in a garden in San Luis Obispo, CA (photo credit: Nancy Starry)

quantitative estimate of the number of monarch butterflies in urban gardens, we surveyed their density in gardens in Berkeley, CA (Supplement S2). If we scale this estimate to all of northern and central California, there would be ~12,000 butterflies in urban gardens. This is <1% of the number of migratory monarch butterflies that overwintered in this part of California in the 20th century. Furthermore, at most about 5% of monarch butterflies survive migration (Supplement S3). Therefore, at the peak of their summer breeding, there were probably at least 20 times as many monarch butterflies throughout the western states as we see in the overwintering groves. In other words, even if we added these urban monarch butterflies to our overwintering counts, and even if we have underestimated the abundance of urban monarch butterflies by an order of magnitude, we still have far fewer monarch butterflies in the West now than we did 3 or 4 years ago.

Another possibility is that the monarch butterfly populations from these urban gardens could themselves be a source of butterflies that would colonise the western states during summer. Again, this possibility seems unlikely. Resident populations of monarch butterflies build up high levels of a protozoan parasite, *Ophryocystis elektroscirrha* (OE), at least in part due to the absence of migratory culling (Altizer et al., 2011). In California, about 8% of migratory monarch butterflies are infected with OE, compared to about 75% of residents (Satterfield et al., 2016). Uninfected monarch butterflies have a tremendous capacity for population increase – a single female monarch can produce 12 adult daughters if milkweed host plants are not limiting (Flockhart et al., 2015) and perhaps three or four daughters under realistic conditions (Supplement S4, Figure 2). This capacity allows monarch butterfly populations to increase rapidly in size during the summer breeding generations. OE-infected monarch butterflies experience lower survival, lower egg-laying rates, and produce about 0.8 adult daughters per female (Supplement S4). If 75% of monarch butterflies have OE, the average rate of increase ($0.75 \times 0.8 + 0.25 \times 3$) is about 1.35 adult daughters per female. This rate of increase is enough for resident monarch butterfly populations to persist in urban areas, but it does not give them the ability to rapidly colonise the other western states. Furthermore, traits associated with migration can evolve rapidly in monarch butterflies (Freedman et al., 2020; Tenger-Trolander et al., 2019). To date, no one has looked for such changes in resident California populations, but they could lose the genetic tendency to migrate, as well as the demographic capacity to do so.

HOW DO RESIDENT AND MIGRANT POPULATIONS INTERACT?

In responding to the current status of western monarch butterflies, one of the greatest uncertainties is how much the resident and migratory populations interact. It may be that the growth of the resident population is independent of the collapse of the migratory one. Monarch butterflies have numerous resident populations worldwide, as well as the migratory ones in North America (Freedman et al., 2020). It could be that climate is becoming suitable for monarchs to live year-round in northern California. It could also be that urban monarch butterfly populations are growing because more people

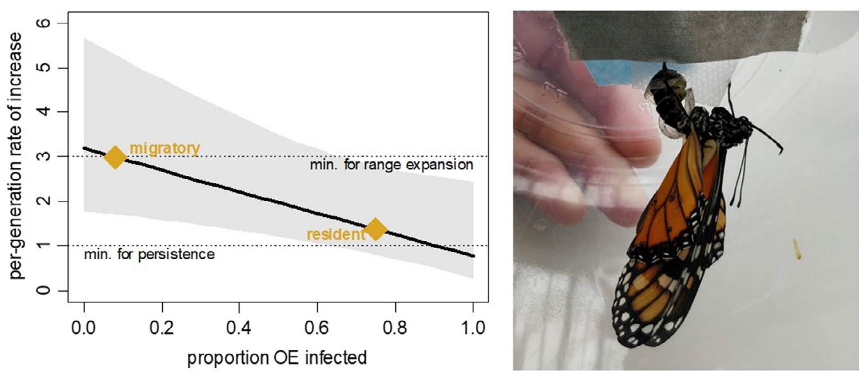

FIGURE 2 Effects of infection by the protozoan parasite *Ophryocystis elektroscirrha* (OE) on monarch butterfly rates of increase during breeding generations. Black lines indicate estimated growth rates (see Supplement S4), with 95% confidence intervals in grey. Points represent values for the estimated proportion of OE-infected monarch butterflies in migratory and resident populations (from Satterfield et al., 2018). Dotted lines identify (1) the minimum growth rate for persistence, set at exact replacement (growth rate of 1 per generation) and (2) an estimate of the minimum growth rate for the population to fill the western states during breeding season (3-fold increase per generation). The growth rate minimum is a rough estimate, justified in at least two ways: First, migratory monarch butterflies have low survival during fall migration, on the order of 2–5% (Supplement S3). If a population increases 3-fold per generation for four breeding generations, the resulting 27-fold increase approximately balances migration mortality. Second, the land area of core western states (California, Nevada, Idaho, Oregon and Washington) is about 527,733 square miles (136,682,847 Ha). If a population starts at 1,000,000 overwintering butterflies (a reasonable historic estimate) and increases to 27,000,000, there would be ~1 monarch butterfly per 5 Ha in its breeding range, which is broadly consistent with its former status as a common species. The photo is of an OE-infected monarch butterfly emerging in the laboratory (photo credit: Christopher Jason, Washington State University)

are planting milkweed in their yards, especially tropical milkweed (*Asclepias currasavica*). Tropical milkweed is a popular horticultural plant, native to South America. Unlike native temperate milkweed species, it provides year-round food for monarch butterflies.

Alternatively, resident and migratory populations could be demographically connected. Perhaps migratory populations are declining because some individuals are attracted to the urban gardens in Fall, instead of migrating to coastal overwintering groves. Perhaps gardens are attractive stopping places in Spring, essentially absorbing butterflies that could have begun recolonising inland sites. If our estimates of population growth rates or infection rates are just a little bit off, then the resident population may be a demographic sink (*sensu* Dias, 1996), in the sense of being sustained only by immigration from the migratory population. In that case, we would expect declines in the migratory population to be followed within a few years by the loss of the resident population.

If populations do interact, a second concern is that the presence of an OE-infected resident population may increase parasite levels in the migratory population. OE is transmitted horizontally on milkweed leaves, and tropical milkweed does not die back in winter. In other parts of the southern United States, migratory monarch butterflies accumulate higher parasite loads when they interact with resident populations on tropical milkweed (Majewska et al., 2019; Satterfield et al., 2018). The potential transmission of OE from resident to migratory monarch butterflies creates a huge source of uncertainty. If the western monarch migration is on the point of collapse, it seems sensible to keep as many individual butterflies alive as possible, including the ones in gardens. However, increasing survival of infected monarch butterflies in gardens could increase parasite transmission to the migratory population (see Ezenwa & Jolles, 2015 for a similar example in a mammal population). For monarch butterflies in California, this kind of negative interaction is possible but by no means certain. It may be that helping monarch butterflies in urban gardens is, in fact, the very best way to sustain monarch butterflies in the West during this critical time. We simply do not know.

RESILIENCE OR CATASTROPHE?

From a conservation perspective, the change in western monarch butterflies presents a conundrum. Even knowing how to implement the precautionary principle of “Do no harm” is not obvious. On one hand, the benefits of milkweed in urban gardens – to public outreach and potentially to the monarch population – are large. On the other hand – if diseased monarchs from urban gardens significantly reduce the likelihood of a robust migration – then there might be real harm.

On the positive side, the appearance of this urban population is a promising sign of how resilient the species might be. In northern California, monarch butterflies have reinvented themselves. To residents of coastal California cities, it must seem like a success to be seeing monarch butterflies in their gardens on a regular basis. It is likely – though not guaranteed – that western monarchs will persist in a small portion of their historic range, even if they are lost from most of it. And yet even this positive note is tinged by the knowledge that we are losing something incredible. Monarch migration has long been recognised as a possibly endangered phenomenon (Brower & Malcolm, 1991; Wells et al., 1983; Wilcove & Wikelski, 2008). The overwintering clusters that used to occur in California are a spectacular phenomenon, and we may completely lose monarch butterflies from the interior West.

Perhaps the most striking feature of these changes is how quickly they happened. By the time we resolve enough uncertainty to provide clear management guidelines, the system may have shifted again. When Doak et al., (2008) concluded that surprises are common in ecology, most of the examples they pointed to were small-scale surprises in experiments, and often on time scales that aligned much more with the time scales of research or management. In hindsight, it may not be surprising if urban gardens are used by butterflies in new ways (cf. Halsch et al., 2020; Hobbs et al., 2009), but changes during the past few years were still startling and unexpected (cf. Crone et al., 2019; Espeset et al., 2016). One lesson from western monarchs is that, in this rapidly changing world, we should expect some species to change quickly and in completely unexpected ways.

CONCLUSIONS

In the West, the migratory population of monarch butterflies is collapsing. Based on available information, a new resident population seems to be expanding in urban gardens. Our assessment is that the resident population is much smaller and is unlikely to replace the migratory one. One could assume that the resident population is a conservation success or, alternatively, a cause of the decline of monarch migration in the West. In fact, we do not know if either of these is true. This startling transition emphasises the general need to be prepared to rapidly reorient conservation policies and practices in changing environments.

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AUTHORSHIP

This viewpoint was drafted by E.E.C., based on conversations with C.B.S. Both authors edited the manuscript, and its final content represents our joint opinion. Supporting analyses, calculations and urban monarch surveys were conducted by E.E.C., and reviewed by C.B.S.

PEER REVIEW

The peer review history for this article is available at https://publons.com/publon/10.1111/ele.13816.

DATA AVAILABILITY STATEMENT

Should this manuscript be accepted, unpublished data for supplementary analyses will be archived in Dryad. Data for supplemental analyses are available from the Dryad Digital Repository: 10.5061/dryad.fqz612jsb (Crone & Schultz, 2019).

ORCID

Elizabeth E. Crone https://orcid.org/0000-0002-5287-221X

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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