U.S. Geological Survey Cooperative Research Units Program: Status Report on Scientific Research on the Monarch Butterfly (*Danaus plexippus*)

Jennifer M. Mock[1] and Jonathan R. Mawdsley[2]

1. JMS Natural Resource Strategies
2. U.S. Geological Survey, Cooperative Fish and Wildlife Research Units Program

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For additional copies or information, contact:

Jonathan Mawdsley
U.S. Geological Survey
Cooperative Fish and Wildlife Research Units
E-mail: jmawdsley@usgs.gov

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Cover photo: Monarch butterfly on showy milkweed at Seedskadee National Wildlife Refuge, Wyoming. Tom Koerner/U.S. Fish and Wildlife Service

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Call for Research on Monarch Butterflies (*Danaus plexippus*)

Jennifer Mock and Jonathan Mawdsley

The U.S. Geological Survey's Cooperative Fish and Wildlife Research Unit Program (USGS, CRU) dates back to 1932 when the first Cooperative Wildlife Research Unit was founded at Iowa State University by noted conservationist and cartoonist Jay "Ding" Darling. The program was expanded into a network of Units in 1935 when eight additional units were created by Congress with the support of a broad spectrum of conservation organizations and agencies. The program since its beginning has focused on delivering world-class graduate education in fisheries and wildlife sciences, conducting applied scientific research, and providing technical assistance to collaborators and partners. Each Unit is a formal partnership between USGS, U.S. Fish and Wildlife Service (USFWS), the relevant state fish and wildlife agency, the host university, and the Wildlife Management Institute (WMI). In the 92 years since 1932, the program has expanded into a network of 43 Units in 41 states, with 104 scientists, some 500+ students, and an additional 500 or more technical and support staff.

Unit scientists strive to communicate results of their research to their program partners and cooperators in a timely manner. In 2021, CRU initiated a project to evaluate State data management and conservation decision-making needs [Big Data Project (BDP), Grant # G21AC10344], through a cooperative research agreement between the CRU program and the Wildlife Management Institute. During discussions about the BDP, the USGS CRU program answered a call from Directors of State fish and wildlife agencies during the CRU's All-Hands Meeting in February 2022 to initiate research collaboratives that help CRU cooperators address science priorities across state boundaries, regions, habitats, and landscapes. Through the BDP's activities, a pilot research collaborative on native pollinators was established and the monarch butterfly was identified as its first species of interest.

Research collaboratives are one of the novel pilot steps to modernize the CRU program in response to this call from State Directors and to meet USGS leaders' direction and priorities. Research collaboratives are one method for the CRU Program and its cooperators to tackle landscape science and research questions that span beyond one state's boundaries, are too complex for one Unit to manage individually, and benefit from CRU scientists in different Units working together. We propose that this approach will help answer large, real world scientific questions in a fashion that continues to support the existing CRU scientific research and student training model. It also facilitates experimenting with the publication of expedited information needed by cooperating partners for near-term decision making. Subsequently and as part of the BDP, the CRU Headquarters and several state agency partners are incentivizing and enabling these regional and multistate activities and research collaboratives in addition to long-standing CRU priorities.

The CRU Program has a long and distinguished history of supporting landscape-level science, from the earliest days of the GAP Analysis Program to the Western Migration Corridors Initiative With a growing need for science to make decisions on species for which many states do not have sufficient expertise or data, the newest CRU effort has developed a **Pilot Research Collaborative on Native Pollinators**. Many state wildlife action plans and the Midwest Association of Fish and Wildlife Agencies' list of regional species of greatest conservation need identify the conservation of native pollinators and their habitats as priorities.

USGS scientists conduct research on North American pollinators whose existence affect ecosystem health and productivity, agriculture, and the survival of other various plants and animals. At the request and interest of a few State Directors, the Pilot Research Collaborative on Native Pollinators focuses first on the monarch butterfly and research questions about the large amount of scientific and peer-reviewed data and information available today on the Monarch butterfly. According to Google Scholar, there were over 5,790 peer-reviewed journal articles published since 2019 on the monarch butterfly [search conducted October 24, 2024; keyword search = *Danaus plexippus*]. Historically, analyzing a data set that large would be very time consuming and difficult. However, with scientific expertise to conduct different analyses today that were not possible 20 years ago, CRU scientists are working together to help their cooperating partners assess that large body of science to inform conservation decisions and future investments as well as contribute to the growing body of scientific knowledge on the monarch butterfly and other native pollinators in the future. For example, a recent study published by the Maine Cooperative Fish and Wildlife Research Unit developed and assessed two model validation methods that can help CRU cooperating partners prioritize surveys of roosting sites as well as conservation efforts during the monarch's fall migration on the Atlantic migration route (Boxler et al., 2024; summary on page 5).

This pilot effort is a multigovernmental, multistate, multiregional research collaborative effort between the USFWS, State fish and wildlife agencies with a strong history of monarch conservation, and USGS CRU program scientists in Headquarters, Missouri, and Nebraska who collaboratively evaluated particular interests within the large body of monarch butterfly literature. This research collaborative also includes scientists with genomic, modeling, and meta-analysis expertise and access to other critical expertise in pollinator biology, lepidoptera population dynamics and genomics, population modeling, data analysis, and other related disciplines, all of which work together to inform state and federal wildlife administrators' decisions on the conservation of the monarch butterfly.

From the large body of data available, State cooperators initially identified the following questions which became the foundation of the Pilot Research Collaborative on Native Pollinators as part of the BDP:

> *What does the voluminous peer-reviewed scientific literature published since the monarch was designated as warranted but precluded under the ESA in 2019 tell us about the status of the species? What important scientific discoveries since 2019 are pivotal to understanding today's status of the species and subsequent actions of managers?*

Specific research projects identified from these questions are the foundational basis for this research collaborative and early results published herein, which includes the following:

- Can we use monarch genomics to verify claims of population decline since 1994 and what else does the monarch genome tell us?
- What does the monarch butterfly's fecundity tell us about the species' resiliency?
- What does the abundant body of peer-reviewed literature tell us about the effects of pesticides and the effects of habitat manipulation on the monarch butterfly?

As conversations continue to develop and priorities emerge from the research collaborative on native pollinators, other plans may emerge to more fully develop this research collaborative and benefit our cooperating partners, USGS scientists, and students. This will be determined and prioritized by cooperating partners and would likely involve species such as native bees and other butterflies for which research is needed to inform state and federal agencies' decisions.

Research collaboratives are intended to assist the cooperating partners with multistate, regional, and landscape-level fish and wildlife science issues, and the CRU Program continues to look for other opportunities to meet the science needs of the cooperating partners. The CRU Program looks forward to working with cooperators to identify and develop additional research collaboratives around uniting issues such as wildlife diseases, structured decision-making, big data analyses, fish and wildlife diversity species management, eDNA, genomics, and others.

Summary of Boxler et al. (2024): Atlantic Flyway Monarch Butterfly Roosts

Boxler, B. M., C.S., Loftin and W.B, Sutton. 2024. Monarch butterfly (*Danaus plexippus*) roost site-selection criteria and locations east of the Appalachian Mountains, U.S.A., Journal of Insect Behavior 37:22-48 https://doi.org/10.1007/s10905-023-09844-5

Cyndy Loftin, U.S. Geological Survey, Cooperative Fish and Wildlife Research Units Program

Monarch butterflies migrating southward along the Atlantic coast in the late summer-early fall are known to rest in roosts nocturnally, however, the characteristics of landscapes where these roost sites occur are not well understood. We used two species distribution modeling approaches to combine citizen scientist-collected observations of roosting monarchs with environmental variables that describe the roost site landscape context to predict potential suitability of lands in the Atlantic flyway for roosting monarchs. Important environmental variables in the roosting landscape included nearness to surface water, high elevation, and vegetative cover. The models were in general agreement in identifying similar areas in the Atlantic Coastal Plain and Appalachian Mountain ridges that contained the greatest amount of potential roosting habitat, accounting for <3% of the study region. This research provides a framework for landscape conservation planning for monarchs migrating in the flyway as well as reveals limitations of available spatial environmental data for habitat conservation that potentially benefits many species, including monarchs.

Synopsis of A Systematic Review of Direct Effects of Pesticides and Other Grassland Management Practices on the North American Monarch Butterfly (*Danaus plexippus*)

Elyssa McCulloch, School of Natural Resources, University of Missouri, Elisabeth Webb, U.S. Geological Survey, Missouri Cooperative Fish and Wildlife Research Unit, and Alex Morphew, Missouri Department of Conservation

In 2020 the U.S. Fish and Wildlife Service published the Species Status Assessment (SSA) for monarch butterfly (USFWS 2020) to summarize the best available scientific information on the species in North America. The SSA focused on quantifying the current and historic distribution and abundance of monarch populations, assessed the status and health of current populations as well as factors influencing population health, forecast potential future changes in these factors and monarch population response to these changes and evaluated overall monarch population viability (USFWS 2020). In the time since the SSA was written, over 4,600 science products referencing the monarch butterfly have been published, meaning that substantial amount of new information on the status of monarch population trends, factors that influence monarch populations, and overall monarch population resiliency is now available.

Synthesizing existing knowledge is crucial to understanding the potential long-term impacts of the most common land management practices across the Great Plains on monarch population viability and to provide practical information for agencies responsible for enacting conservation measures on the ground. We reviewed and synthesized empirical literature published on the direct effects of the most common grassland management practices (mowing, grazing, burning, haying) and pesticide (herbicide, insecticide, fungicide) applications on monarchs across all life stages, identified information gaps and uncertainties, and assessed the potential impact of these management practices on future monarch population viability. We reviewed the literature published from 2019-2024 to include information after the publication of the 2020 USFWS Species Status Assessment and focus on research that investigates direct effects on monarch butterflies at any life stage. We also reviewed the potential for cumulative effects across life history stages and synergistic effects of management practices.

We conducted a systematic review following the Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) guidelines and developed a protocol to document the process, outlined briefly below (Page et al., 2021). We used three citation databases to search the primary literature for empirical studies published in scientific journals, books, or conference proceedings, as well as Master theses and Doctoral dissertations from 2019-2024 and followed a set of predefined eligibility criteria (Table 1). Next, we systematically screened these publications by reviewing the title and abstract of each paper to assess relevance to the topic. Then we conducted a full-text review of the remaining records and included or excluded those based on methodology. Following the protocol resulted in a combined 714 records using the two search strings across three databases. Records fitting our search criteria comprised approximately

6% of the overall monarch literature published since 2019. Next, we removed 219 duplicate products across databases and screened the remaining 495 titles and abstracts for relevance to our objective. The largest number of records were excluded in this step (n = 452) leaving 43 records relevant to our objective to screen for full-text availability and further eligibility criteria. All 43 records had full text available, but 15 did not meet our criteria for inclusion or were thesis or dissertations of which the relevant chapters had been published and collected by our search methods. This resulted in 28 relevant articles to our objective.

Table 1. Number of results from the selected search string and database combinations

	Results		
Search String	**Google Scholar**	**Web of Science**	**Scopus**
(monarch OR “monarch butterfly” OR “danaus plexippus”) AND (habitat* OR grassland* OR landscape*) AND (mow* OR graz* OR burn* OR disturbance OR manage*)	1020*	69	61
monarch* OR "monarch butterfly" OR "danaus plexippus" AND (herbicide* OR pesticide* OR fungicide* OR insecticide*)	2330*	3828*	57

Asterisks indicate search results from which only the first 200 records were reviewed. Unavailable papers were not included. Final number of records reviewed was 714.

Among the collective studies included in our review, all monarch life stages were studied, with the most comprehensive evaluation of the adult stage. Only two studies meeting our criteria assessed the effects of grassland management on monarchs, whereas the remaining 26 studies evaluated the direct effects of pesticide use on monarchs or aimed to quantify monarch pesticide exposure. Although the SSA highlights monarch conservation best management practices that prioritize increasing milkweed and diverse nectar resources, it lacks information pertaining to the direct effects of grassland management strategies on monarch populations. This overall information gap was highlighted in-this review, which identified only two empirical studies examining how grassland management impacts monarch fitness[1] or survival. Both studies found that the effects of grassland management practices were indirect, mediated through changes in

[1] Fitness is any endpoint measured regarding the whole-organism performance including the health of the individual (Brownscombe et al., 2017; Orr & Garland, 2017).

Brownscombe, J.W., Cooke, S.J., Algera, D.A., Hanson, K.C., Eliason, E.J., Burnett, N.J., Danylchuk, A.J., Hinch, S.G. and Farrell, A.P., 2017. Ecology of exercise in wild fish: integrating concepts of individual physiological capacity, behavior, and fitness through diverse case studies. *Integrative and Comparative Biology*, *57*(2), pp.281-292

Orr, T.J. and Garland, T., 2017. Complex reproductive traits and whole-organism performance. *Integrative and Comparative Biology*, *57*(2), pp.407-422.

host plants or nectar availability. Specifically, monarchs preferentially oviposit on mowed milkweed, depending on the time of year in relation to peak monarch abundance (Knight et al., 2019). Most published research assessing the impacts of grazing and burning on butterfly communities has primarily been conducted in Europe, where grassland butterfly declines are well documented, and conservation efforts are more advanced (Warren et al., 2021).

Recent studies have begun to reveal the widespread exposure of monarchs and other insects to pesticides in agricultural areas through consumption of milkweed and nectar contaminated at sublethal levels (James, 2024; Wagner, 2020). The response of monarchs to pesticide exposure can be highly variable and depends on monarch life stage, pesticide family, application method, and location and proximity of the monarch relative to the pesticide application area. However, of the 26 studies that tested the direct effect of pesticides on monarchs or exposure potential, 18 indicated pesticides had a negative effect on at least one, if not multiple, monarch fitness metrics at a specific life stage (James, 2019; Knight et al., 2021; Krishnan et al., 2020, 2021a). Immature monarchs (i.e. eggs, larvae, pupae) include the life stage most susceptible to lethal effects from acute and chronic pesticide exposure (Krishnan et al., 2021b). Recent studies have begun to reveal the widespread exposure of monarchs and other insects to pesticides in agricultural areas through consumption of milkweed and nectar contaminated at sublethal levels (James, 2024; Malcolm, 2018; Wagner, 2020). Pesticides have been detected on milkweed leaves, within leaf tissues, and even in the nectar of milkweed flowers and other nectar resources (James, 2024; Naujokaitis-Lewis et al., 2024). Both acute and chronic exposure have been shown to cause high mortality rates and a range of sublethal effects, which have severe demographic consequences for monarchs across their multiple life stages. Acute exposure to reactive insecticides, such as organophosphates, pyrethroids, and diamides, results in the greatest mortality rates across monarch life stages (Giordano et al., 2020; Grant et al., 2021; Krishnan et al., 2021b).

While acute exposure risk may be relatively low, chronic exposure to insecticides, particularly neonicotinoids, is likely high and can lead to long-term sublethal effects and prepupal mortality. These effects can include impaired growth, delayed development, and altered reproductive behavior, all of which impact monarch survival and reproduction. Studies have shown that neonicotinoids accumulate in milkweed plants, leading to sublethal impacts on caterpillars reared on contaminated foliage (Bargar et al., 2020; Naujokaitis-Lewis et al., 2024). Caterpillars that ingested milkweed contaminated with neonicotinoids also exhibited reduced growth and delayed development, resulting in smaller, lighter adults (Bargar, 2024; Bargar et al., 2020). The impacts of neonicotinoids extend further to adult monarchs, reducing longevity and flight metabolic rate and altering reproductive behavior (Cibotti et al., 2024).

Fungicides are often overlooked in discussions of pesticide impacts, despite their critical role in agriculture and plant protection. While only 6 studies in this review examined effects of fungicides on monarchs, the collective findings suggest substantial risks to monarch population viability, highlighting how increased attention to this class of chemicals could further understanding. Fungicides can be highly toxic to non-target organisms because they target basic biological processes that are not exclusive to fungi.

While this review highlights a growing body of work investigating effects of pesticides on monarchs in the Midwestern United States, and some representation in the Northeast and Southeast, there is an apparent lack of research on this topic from the Southern United States where migrants traverse before they overwinter and return to as a final stop to lays eggs for the next summer breeding generation. This information gap is particularly important as recent evidence points to spring monarch abundance as a strong predictor of overwintering counts (Zylstra et al., 2021). Data gaps in pesticide use at management-relevant scales (e.g., county level), combined with growing evidence of pesticide persistence and its threat to insects, highlight how additional ecologically relevant metrics and monitoring could help inform regulation of environmental chemical, and characterization of contamination of milkweed and nectar resources (Bargar, 2024; James, 2024; Yang, 2023).

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Summary of Population Genomic Research on North American Monarch Butterflies

Sarah Sonsthagen, U.S. Geological Survey, Nebraska Cooperative Fish and Wildlife Research Unit

North American monarch butterflies (*Danaus plexippus*) are a charismatic pollinator, in part, because of their unique continent-scale migration that spans multiple generations and the formation of large dense clusters of individuals at winter roost sites (Gustafsson et al. 2015). Migratory segments of North American monarch butterflies occupy different geographic regions, east and west of the Rocky Mountains, throughout the annual cycle with the eastern segment comprising a majority (2-3x magnitude greater) of monarch butterflies (Freedman et al. 2021). Western North American monarch butterflies overwinter at numerous sites along coastal areas of California and Baja California. Eastern North American monarch butterflies overwinter in the Transverse Neovolcanic Range of central Mexico. Eastern and western segments of North American monarch butterflies differ in migratory behavior. The eastern North American segment migration is 6x longer in duration and approximately 3-4x farther in distance (eastern 1,500–3,000 km with some 4,000 km, Flockhart et al. 2017; western <800 km with maximum distance 1,400 km, James and Kappen 2021). Flight trials have also demonstrated differences in performance between eastern and western segments of North American monarch butterflies that are reflected in wing morphology (Talla et al. 2020).

The unique multigenerational migration displayed by monarch butterflies coupled with non-migratory populations has spurred considerable research in the genetic underpinnings of innate migratory behavior (see reviews by Merlin et al. 2020, Freedman et al. 2023). Comparisons among populations with differing movement strategies identified divergent selection at 536 genes hypothesized to be involved with migratory behavior and associated diapause (Zhan et al. 2014, Merlin et al. 2020, Freedmen et al. 2023). Analysis of eastern and western North American monarch butterflies involved in flight trails, identified differential gene expression at one of the six candidate genes associated with nonmuscular motor activity (Talla et al. 2020). As candidate loci were selected because of their association with migration-related genes during active flight, differential expression of other genes in regulatory networks involved in migration behavior, wing morphology, and reproductive diapause likely exist between eastern and western segments of North American monarchs and warrants future research.

Morphological and behavioral differences between eastern and western segments of North American monarch butterflies, however, are not reflected in the genome-wide assessments of differentiation. Several studies have assessed genetic structure within North American monarch butterflies (Brower and Boyce 1991, Shephard et al. 2002, Lyons et al. 2012, Zhan et al. 2014, Talla et al. 2020, Hemstrom et al. 2022). Earlier work employed allozyme (Brower and Boyce 1991, Shephard et al. 2002) and microsatellite (Lyons et al. 2012) data sets to evaluate genetic structure between eastern and western segments of North American monarch butterflies. More recent studies analyzed whole genome (Zhan et al. 2014, Talla et al. 2020) and reduced representation (Hemstrom et al. 2022) sequence data. Results were congruent across marker types. No genetic differentiation was detected within North America migratory segments and whole genomes were only 0.1% diverged (Talla et al. 2020). Tagging data have identified movement between eastern and western segments. Of the 3194 western monarchs tagged in Arizona, 32 were recovered in California overwinter sites and 12 were recovered in Mexico (Billings et al. 2019). As breeding occurs in spring at overwinter sites, any abmigration by individuals would provide avenues of gene flow between eastern and western segments of North American monarch butterflies and promote panimixia within migratory forms. Although differential gene expression was detected, genetic diversity was nearly identical across chromosomes, no fixed differences in nucleotide base pairs were observed, and no islands of differentiation were identified (highest F_{ST} observed was 0.060 at 100 base pair sliding window; Talla et al. 2020). Phenotypic differences in behavior, flight, and morphology, therefore, likely have an environmental basis or are the result of a large number of small-effect alleles (Talla et al. 2020). While sample sizes are appropriate for studies using whole genome (N=14 eastern, N=29 western; Talla et al. 2020) and reduced representation genome (N=45 eastern, N=40 western; Hemstrom et al. 2022) sequence data, evaluations of species that exhibit subtle structure may benefit from increased sample sizes to uncover small effect alleles that may be responsible for differences between regions and among individuals displaying divergent migratory behaviors.

Over recent decades, monarch butterflies have increasingly become the focus of conservation concerns. Both the eastern and western segments of North American monarch butterflies have experienced marked population declines. The western North American segment count data estimate a >99% reduction in abundance of overwintering monarchs (James et al. 2024). Although declines in the eastern segment are not as marked (>80%; Semmens et al. 2016), reduction in the area occupied at winter roost sites in Mexico may have started as early as the mid-1970s (Zylstra et al. 2020). While causes of decline have yet to be identified, illegal logging at the overwinter sites, climate change, reduced availability of nectar sources during migration, and agricultural practices (e.g., loss of milkweed host plants and pesticide use) are posited as stressors to butterfly populations (Talla et al. 2020 and citations therein). Recent work implicated insecticides, and specifically neonicotinoid-treated seeds, as a potential driver of declines as the shift in insecticide application is more associated with reduction in abundance in monarch butterflies than climate and land use (Van Deynze et al. 2024).

The marked decline in North American monarch butterflies prompted concerns about the persistence of the unique behavioral segments of the species and the capacity of monarch butterflies to respond to current and emerging threats. The effective population size, thereby retention of genomic diversity, underlies a species and populations' ability to respond to stressors in the environment at both current and future conditions. Dramatic reductions in census sizes not only reduce the capacity of populations to retain genomic diversity but also allow for the expression of deleterious mutations that are present in the population at low frequency, which can further erode the viability of populations in decline. The relatively large effective population sizes estimated for North American monarch butterflies ($N_e = 2 \times 10^6$; Zhan et al. 2014) and congruence in estimates between eastern and western segments (Talla et al. 2020) suggest that North American monarch butterflies were able to retain genomic diversity through recent declines, and therefore, evolutionary potential to respond to current and emerging stressors. Evidence identifying insecticides as drivers of monarch butterfly abundance (Van Deynze et al. 2024) and inference a that declines were likely already occurring in the North American eastern segment in 1970s (Zylstra et al. 2020) suggest that the declines observed since the early 2000s may not have been the first that monarchs experienced in the past century. Assessments of genomic diversity based recent samples fail to capture evolutionary potential lost due to previous declines associated with stochastic weather events, agricultural practices, or other mechanisms. Information regarding how past changes in census size have influenced standing levels of genomic diversity could help to more fully evaluate the resiliency of the North American monarch butterfly to ongoing and future stressors.

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Factors Contributing to Resilience in the Monarch Butterfly, *Danaus plexippus*: Some Considerations and Context

Jonathan Mawdsley

The monarch butterfly, *Danaus plexippus* L. (Insecta: Lepidoptera), is currently a species of conservation interest, due to reported declines in overwintering populations in México and the United States (Thogmartin et al. 2017). These declines have been attributed to various factors such as changes in land use, agricultural chemical applications, and deforestation at overwintering sites, among others (Thogmartin et al. 2017). However certain attributes of this species suggest that it may exhibit a considerable degree of resilience in the face of certain threats and stressors. The purpose of this note is to provide context regarding various factors which may contribute to resilience in this species, using information from the peer-reviewed scientific literature.

Fecundity. Monarch fecundity appears to be high relative to other butterfly species and may have been underestimated in the past. Oberhauser (1997) studied lifetime egg production of 47 female monarch butterflies and reported an average of 715 eggs laid per female, with minimum 290 eggs and maximum 1179 eggs. These numbers contrast with those reported by Ehrlich and Ehrlich (1978), who dissected females of 300 different butterfly species (including *Danaus plexippus*) from multiple continents representing 14 family-level taxa. Those authors reported that no species of butterfly they examined (including monarchs) had more than 200 eggs in any single ovary (with a pair of ovaries in each female butterfly; Ehrlich and Ehrlich 1978). The relationship between eggs in ovaries and lifetime egg production in monarchs is not well understood, but the Oberhauser (1997) study suggest that lifetime egg production can be greater than the total number of eggs present in the ovaries at a particular point in time (Ehrlich and Ehrlich 1978; Chew and Robbins 1984). Indeed, monarch fecundity may very well have been underestimated in the past, based on estimates derived from dissections alone.

In the context of the Ehrlich and Ehrlich study, the monarch fecundity reported by Oberhauser appears to be high relative to other butterfly species. Indeed, actual counts of eggs laid by individual female butterflies of other taxa approach monarch levels only in widespread and invasive species such as the small or cabbage white *Pieris rapae*, in which female egg production is reported to be 400-1000 eggs per female (Suzuki 1978; CABI 2019; Konno 2023). High levels of egg production, relative to other butterfly species, appear to be a property of at least some monarch populations.

Number of generations. Migratory populations of monarch butterflies have four to five generations per year (Oberhauser and Solensky 2004). In contrast, the majority of temperate zone butterfly species undergo one to three generations per year (Scott 1992; Altermatt 2009). In certain butterflies, increases in the number of generations can help drive population increases and promote overall resilience, particularly in highly fecund species such as the cabbage white

(*Pieris rapae*) where the addition of generations can help to drive a "multiplier effect" with increasing numbers of butterflies in each generation (Konno 2023; Forister et al. 2023). Climate change is thought to be increasing the number of annual generations in temperate butterfly species in Europe, although this may not necessarily result in increased fitness for individual species. (Altermatt 2009)

Geographic distribution. Monarch butterflies have been recorded from 90 countries, islands, and island groups worldwide, many of which represent recent colonization events in the past two hundred years, some of which may have been mediated through human activities (Nail et al. 2019; Freedmen et al. 2020). Only a few other butterfly species have such broad global distributions, notably the painted lady *Vanessa cardui* (Shields 1992) and the cabbage white *Pieris rapae* L. (Konno 2023). As noted by Nail et al. (2019), the large number of individual populations of monarch butterflies worldwide, many of which have been established in the past two hundred years (Freedmen et al. 2020), provides a degree of redundancy and resiliency for the species overall, thereby reducing the likelihood of a global extinction of the species as a whole.

Survival of past catastrophic events. *Danaus plexippus* is thought to have separated from closely related species in either the Miocene (Aardema and Andolfatto 2016) or Pliocene (Lushai et al. 2003). As such, the species has experienced and survived a number of significant global disruptions, including the multiple Pleistocene glaciations, the "Little Ice Age" and the "Medieval Warm Period," and most recently, the "Dust Bowl" of the 1930s. The major glaciations would have covered most of the geographic area in central North America which is now considered to be the major production area for migratory monarch butterflies in the Midwest (Šibrava 1986; Syverson 2011), as mapped by Thogmartin et al. (2017). It is worth noting that much of the area producing migratory monarchs in the upper Midwest at present would have been covered by continental scale glaciers as recently as 12,000 years ago (Šibrava 1986; Syverson 2011). Likewise, the "Dust Bowl" affected substantial areas of the central United States which today support migratory populations of the monarch butterfly (Murphy 1935), as mapped by Thogmartin et al. (2017). The effects of the "Dust Bowl" on specific monarch butterfly populations are unclear, although the examination of genetic and genomic information from preserved museum specimens could shed light on population dynamics of the species under these altered environmental conditions.

The argument that monarch butterflies survived these major global and regional events is strictly inferential at the present time, based on the estimated divergence time for the species and the species' presence in the affected areas. One of the principal objectives of research underway at the USGS Nebraska Cooperative Fish and Wildlife Research Unit is to determine whether or not these significant continental and global change events have left signatures on the genome of the monarch butterfly, evidence which may in turn provide managers with potentially useful information regarding the resilience of the species to disruptions.

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Surveying a Vast Literature: Opportunities to Inform Conservation of the Monarch Butterfly, *Danaus plexippus* L. (Insecta: Lepidoptera)

Jonathan Mawdsley

There has been considerable interest across many sectors of society in the conservation of the monarch butterfly *Danaus plexippus* L. (Insecta: Lepidoptera) since a proposal to list the species under the U. S. federal Endangered Species Act was released in 2014 (Thogmartin et al. 2017). Scientific research on the monarch butterfly is one of these areas of expanded interest; the online "Google Scholar" database (https://scholar.google.com accessed October 24, 2024) of scientific and technical publications shows over 18,000 records for the search terms "Danaus plexippus" for all time, with some 5,790 of those records published since 2019 alone.

These recent scientific and technical publications cover many subjects which are relevant to our understanding of the butterfly, its population status, and its conservation. Here for consideration are the total numbers of database citations for the period 2019-2024, for particular combinations of search terms, as of October 24, 2024.

"Danaus plexippus" and "population dynamics" – 871 citations

"Danaus plexippus" and "population genetics" – 275 citations

"Danaus plexippus" and "extinction risk"- 330 citations

"Danaus plexippus" and "conservation" – 3,390 citations

"Danaus plexippus" and "conservation status" – 321 citations

"Danaus plexippus" and "habitat requirements" – 251 citations

"Danaus plexippus" and "pesticides" – 1,210 citations

"Danaus plexippus" and "climate change" – 1,830 citations

"Danaus plexippus" and "migration" – 2,280 citations

"Danaus plexippus" and "population model" – 148 citations

"Danaus plexippus" and "fecundity" – 940 citations

"Danaus plexippus" and "mortality" – 1,810 citations

Many of these recently published scholarly documents undoubtedly offer additional insights into the biology of the monarch butterfly. Other citations may simply mention the species in passing or mention it as a reference point in discussions of other species or in discussions of various ecological phenomena.

To examine the degree to which these new records present new and meaningful information about the monarch butterfly and its biology, I used Google Scholar to identify publications which included information about the number of eggs laid by female monarch butterflies in either field or laboratory settings. This information can in turn be compared to data published in a classic benchmark study by Oberhauser (1997) which presented data indicating that female monarch butterflies laid between 290 and 1,179 eggs, with average of 715 eggs per female.

A search with the terms “Danaus plexippus” and “number of eggs laid” conducted on October 24, 2024, yielded 180 results. Further refinement of the search to the terms “Danaus plexippus” and “number of eggs laid per female” yielded 21 results, of which four were focused on Danaus plexippus (the others focused on egg production in other insect taxa). The two published papers provided valuable information and context for egg production and survival in monarch butterflies. Prouty et al. (2023) reported total egg numbers in the 100-200 range for most of the captive butterflies in their study, and also reported declines in total egg numbers laid as a function of increasing exposure to neonicotinoid insecticides. Solis-Sosa et al. (2021) reported monarch oviposition rates in terms of number of eggs per female per day, with a minimum of 0 and a maximum of 52. Both results appear commensurate with results reported by Oberhauser (1997), recognizing that Prouty et al. (2023) and Solis-Sosa et al. (2021) were measuring egg production for time periods shorter than the total lifetime of the butterflies they studied. The other two records recovered were Masters theses, one of which was later published as Prouty et al. (2023) and the other of which remains unpublished.

The Prouty et al. (2023) study raises interesting questions about the effects of pesticides on egg production in monarch butterflies. Adding the search term “pesticides” to the original search string above (“Danaus plexippus” plus “number of eggs laid” and now “pesticides”) resulted in 60 results, many of which appear to be publications focused on examining the effects of individual pesticide chemicals on aspects of monarch butterfly biology such as fecundity and mortality. Replacing “pesticides” with “neonicotinoids” yields 26 results, each of which examines effects of particular insecticides on monarch butterfly demographic parameters. Although these are generally laboratory studies, this body of literature could be used to help scope further laboratory and field studies of pesticide effects on monarch butterflies.

Based on these initial findings, further investigation of citation databases appear likely to yield additional management-relevant information about the monarch butterfly. The contents of this database provide opportunities for researchers to obtain recent scientific information on this species and important threats to its survival, facilitating additional studies such as literature reviews, meta-analyses, syntheses and field studies.

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