Journal of Insect Conservation (2023) 27:181–191
https://doi.org/10.1007/s10841-022-00433-z

ORIGINAL PAPER

What do monarchs feed on in winter? Nectar sources at hibernation sites

Nancy Sánchez-Tlacuahuac[1] · José Luis Pimentel-Equihua[2] · Vicente Espinosa-Hernández[3] · Heike Vibrans[1]

Received: 30 May 2022 / Accepted: 7 September 2022 / Published online: 4 November 2022

Abstract

Introduction The steep population decline of the emblematic monarch butterfly is caused mainly by the reduction of food sources for caterpillars and adults, as well as disturbance in its overwintering forests. Although feeding at the overwintering sites in Mexico has long been considered unimportant, observations show that butterflies feed inside and outside of their forests on sunny days. Nectaring close to the hibernation colonies may be relevant for their conservation, as their reserves decline faster in disturbed forests. However, there are no systematic studies on nectar sources in the Monarch Butterfly Biosphere Reserve, Michoacán, Mexico.

Aims In this study, we identified and quantified the main plant species visited by butterflies for nectaring in the Reserve.

Methods We collected systematic observational data on the flora and butterfly visits in three sanctuaries, around colonies formed between February and March of the 2019–2020 season.

Results Butterflies fed on 29 plant species from 10 families. Most had white, yellow or blue flowers, were somewhat synanthropic and had their main flowering season in winter. The most visited species were *Salvia mexicana* and *S. plurispicata*, which were also the most abundant. By individual plant, *Prunus serotina*, *Crataegus mexicana*, *Buddleja sessiliflora*, *Verbesina oncophora* and *Roldana albonervia* were the most visited.

Discussion/Implications for insect conservation The results point to possible interventions in support of the butterflies. The visited species are generally easy to encourage or cultivate and could be promoted in the surrounding agricultural areas.

Keywords Overwintering · Pollinators · Nectar sources · Mitigation

Introduction

The monarch butterfly, *Danaus plexippus*, is one of the most emblematic and beloved insect species in the world. This has several reasons: its well-known long-distance, multigeneration migration, its aposematism, that is the capture of toxic substances of plants as defense against predators, and its advertisement of unpalatability with a conspicuous color pattern (Malcolm 1994). However, it is under various threats: the decline in larval food plants in the northern part of its distribution, lack of nectar sources on its migration pathway, forest degradation in the monarch's hibernation sites in Mexico, and climate change (Brower et al. 2002, 2006, 2011; Pleasants and Oberhauser 2013; Rendón-Salinas et al. 2019) .

The monarchs' food sources vary with life stage. Caterpillars feed mostly on milkweeds, species of the genus *Asclepias* (Apocynaceae) (Galindo Leal and Salinas Rendón 2005). After metamorphosis, the butterflies obtain nectar from flowers, drink water or lick decomposing fruits and soil with their proboscis (Escobés and Vignolo 2018). As adults, monarchs search for high-calorie food to convert into energy reserves for long flights, hibernation, search for mates and reproduction (Galindo Leal and Salinas Rendón 2005). Along the migratory route, they feed on a variety of other plants (Brower et al. 2006; Rudolph et al. 2006). In Mexico, for example, they feed on different species of marigold (*Tagetes*), *Lantana camara* or a sunflower-like plant,

✉ Heike Vibrans
heike@colpos.mx

[1] Agroecología y Sustentabilidad, Colegio de Postgraduados, Estado de México, Texcoco, Mexico

[2] Desarrollo Rural, Colegio de Postgraduados, Texcoco, Estado de México, Mexico

[3] Edafología, Colegio de Postgraduados, Texcoco, Estado de México, Mexico

Tithonia tubiformis (CONABIO 2014; SEMARNAT 2018). When the monarchs arrive at their hibernation sites, each individual has an average of 133mg of lipids, and at the end of the season it has 52mg (Alonso Mejía et al. 1995), also Alonso-Mejía et al. (1997).

Early studies stated that nectar consumption at the hibernation areas was unimportant because the numbers of butterflies far exceeded nectar sources (Brower et al. 1977). However, it is unclear if these studies also considered the surroundings of the hibernation sites. Feeding was sufficiently obvious for a group of investigators to study the difference in weight between feeding and non-feeding butterflies; they found that feeding butterflies were mostly severely underweight (Alonso-Mejía et al. 1997; Rendón Salinas 1997). However, they only studied the difference between butterflies nectaring within the forest and those that did not at that moment; apparently, they did not sample the very conspicuous "butterfly rivers" that form under appropriate circumstances (see below). Later, controversy erupted on the importance of winter feeding, with one author proposing to increase disturbance to promote nectar sources (see Hoth 1995) and the responses of Alonso-Mejía et al. (1995) and Brower (1995)). The reply of Brower emphasized the lack of information on these nectar sources and their relative significance but doubted their importance. Alonso-Mejía et al. focused on the importance of dense forests that help monarchs conserve energy, particularly under the occasional extreme weather conditions.

On sunny days - almost daily in the second half of their stay - monarch butterflies will form butterfly "streams" or "rivers" from their hibernation trees to lower-lying open areas; this has been interpreted as a search for water in order to process the lipids. Indeed, the butterflies seek out sources of moisture, but they also take advantage of flowering herbs, shrubs and trees to nectar. There are a number of flowering plants in the fir forests where monarchs hibernate, but even more so in the surrounding cultivated landscapes. Though most herbaceous species reproduce during the rainy season, a number of shrubs and trees of the area, as well as a few herbs, flower in the dry season, i.e., winter (Rzedowski 2006; Cornejo-Tenorio and Ibarra-ManrÍquez 2007). Rendon-Salinas (1997) found various species that may be attractive for the animals, belonging to such genera as *Eupatorium*, *Senecio*, *Stevia* and *Salvia*. So, nectar probably has a supportive function at least. Some other evidence points to the relevance of nectaring in the southern parts of the fall migration range (Brower et al. 2006; Hobson et al. 2020).

Butterflies consume their lipid reserves depending on their activity. Extremes in sunlight, relative humidity and temperature increase in disturbed or open forests. Thus, forest deterioration may deplete energy reserves in the monarchs, and result in fewer survivors with sufficient lipid reserves for mating and the flight back to their breeding grounds (Alonso Mejía et al. 1995; 1997; Brower et al. 2006; SEMARNAT 2018). Nectar sources near the hibernation sites could become more important under these circumstances (Brower et al. 2011).

Despite these observations, there are no systematic studies on the plants visited for nectaring from the Monarch Biosphere Reserve in Mexico. This study identifies the main feeding plants of monarch butterflies in their overwintering sites, separating the effect of plant species identity from species abundance. This information will be useful for forest management. It can also help to make the cultivated landscapes of the region friendlier for these animals by integrating the visited species into agroecosystems, or even for pollinator gardens as local attractions (Rogel-Fajardo et al. 2011; del Coro Arizmendi et al. 2020).

Materials and methods

Study area

The Monarch Butterfly Biosphere Reserve, covering an area of 56,259 hectares with three core (13,551ha) and two buffer zones, is located between the States of Mexico and Michoacán, in Central Mexico. The three core zones are mostly situated above 3,000 m: Cerro Altamirano (588ha in the northern part of the reserve), Sierra Chincua-Campanario-Chivatí-Huacal (9,671ha in the center) and Cerro Pelón (3,339ha in the south). It has a cool to cold subhumid climate with summer rains (C(w2)(w)(b'(i"); SEMARNAT/INECC 1996) and is part of the Trans-Mexican Neovolcanic Belt (Tamayo 1962), with volcanic rock subsoil. The forests of the Reserve are crucial for recharging the aquifers that supply groundwater to the Lerma-Santiago and Balsas hydrological basins, and urban centers such as Mexico City and Toluca (Gutiérrez Carbonell et al. 2001).

The vegetation is composed of oak, pine-oak, pine, fir, cedar and juniper forests, and grasslands (SEMARNAT/INECC 1996); the monarchs hibernate mainly in the fir (*Abies*) forests. Villages and agriculture can be found at lower elevations. The reserve is home to at least 132 bird species, 56 mammals, 423 vascular plant species, and 211 fungi (Díaz Barriga 2002). Some endemic species such as the salamanders *Ambystoma rivulare* and *Pseudoeurycea bellii* (Parra-Olea et al. 2005) are found, as well as other protected species such as the *Pinus martinezii* and *Juniperus monticola* (Rendón-Salinas et al. 2005).

The large number of landowners makes conservation action complex (Gutiérrez Carbonell et al. 2001). Stakeholders include 59 ejidos and 13 Mazahua and Otomí

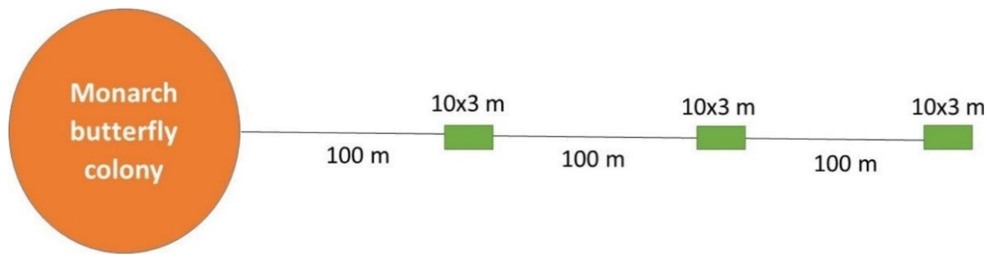


Fig. 1 Diagram of the sampling method. The orange circle represents the butterfly colonies and the green rectangles the observation plots

indigenous communities; both communities and ejidos are forms of legal, communal land ownership in Mexico. There are 21 small properties and some state and federal-owned lands as well. Also, human development is an important goal, as the communities surrounding the Reserve are poor and lack employment outside of subsistence agriculture and seasonal tourism.

Forest degradation and loss of forest cover due to logging and land use changes are evident in parts of the Reserve (Brower et al. 2002). Natural factors such as rains, droughts and strong winds, exceeding the resistance threshold of these ecosystems, have deteriorated their structure and function in recent years (Vidal et al. 2014). An exceptional storm in 2016 substantially reduced the density of the fir canopy (Brower et al. 2017), and was followed by controversial salvage logging (Leverkus et al. 2017). The national and international increase in avocado consumption is a particularly strong incentive for land use change (Burnett 2016), though deforestation within the reserves appears to have declined considerably in the last decade due to better coordination of stakeholders and incentives for landowners (Flores-Martínez et al. 2020).

The investigation took place in a protected area that belongs to three *ejidos*. It was purely observational; we did not need a collection permit. The Reserve authorities were informed in writing of the project, as required. We visited each ejido president and explained the project. They assigned guides who supervised all field work and served as informants.

Selection of the study sites

In February to March 2020, during the period of this study, there were 22 hibernation sites in 15 sanctuaries (core areas) inside and outside of the Reserve (Rendón-Salinas et al. 2020). The colonies were located between 18°59’25” to 19°58’21” N and 98°41’37” to 100°49’ W.

The study sites were selected based on recommendations from local residents and staff from the World Wildlife Fund in charge of monitoring the hibernating monarch butterfly. They recommended working in sites with the largest butterfly colonies, considering occupation constancy and surface area within the forest: (1) Ejido “El Capulín”, Cerro Pelón Sanctuary, municipality of Donato Guerra, State of México, south of the Reserve; (2) Ejido El Rosario, Sierra Campanario Sanctuary, municipality of Ocampo, State of Michoacán, center of the Reserve and (3) Ejido Cerro Prieto, Sierra Chincua Sanctuary, municipality of Angangueo, State of Michoacán, north of the Reserve. The most conserved site with the densest forest was El Rosario, Cierro Prieto was intermediate, and El Capulín had a relatively high level of disturbance and less dense fir forest (WWF-México 2020).

During the 2019–2020 season the monarch butterfly populations occupied a forest area of 2.83 hectares. The colony of the ejido El Rosario covered 1.27ha, Sierra Chincua 0.28ha in the ejido Cerro Prieto, and Cerro Pelón (Colonia de la Comunidad Indígena San Juan Xocunusco, the closest to the ejido El Capulín) 0.28ha (Rendón-Salinas et al. 2020). In the 2020–2021 season the occupied area was 2.10ha, of which 0.73ha was located in El Rosario, 0.07ha in Cerro Pelón and there were no area records for the ejido Cerro Prieto (Rendón-Salinas et al. 2021).

To find the initial sampling locations, we asked knowledgeable local people, such as tour guides, about butterfly movements on sunny days. Most flight corridors were near streams, creeks and ravines, but also in some flat places. Sampling sites were placed close to the overwintering colony within the sanctuaries (“inside”) and downstream of the flight corridors, outside of the sanctuary in sometimes more disturbed places (“outside”).

Field methods

The feeding butterflies were observed on plots along transects for predetermined time periods (Matteucci and Colma 1982; Bautista Zúñiga et al. 2011); this is a common technique for documenting pollinators. In each of the three sanctuaries, we placed two transects with three observation plots each. For the first transect, the first 10×3m observation plot was located 100m from the colony and in the direction of the flight corridor. Another two observation plots were positioned at distances of 100m in the same direction (Fig. 1). Then, we searched for an appropriate and accessible site approximately 1km along the flight corridor, and again, three observation plots were placed there at 100m intervals. The size of the observation plots was based on pilot evaluations and considered the size of most flowering plants (mostly shrubs and some herbs), observable area, butterfly movement, floristic variation, and vegetation heterogeneity.

Observations on the feeding plants of the monarch butterfly initiated on February 11 and ended on March 13, 2020. These dates were chosen because they had reliable sunshine almost daily. Weekly field visits started on February 11 in "El Capulín", February 12 in "Sierra Chincua" and February 13 in "El Rosario"; each transect was visited seven times on sunny days (February 11–13, 17–19, 23–25, 26–28; March 4–6, 8–10, 11–13).

During the first visit, the plots were marked with string, and the coordinates noted. The observer then stood outside of the plot and watched butterfly movement. Flowering plant species on which the monarch butterflies posed and inserted their proboscis into the flowers were considered nectar sources or feeding plants. The individual plants of these species were numbered, measured (larger plants) or estimated based on a few measurements (dense populations of smaller plants, particularly *Salvia*): height and largest diameter, from leaf tip to leaf tip.

The species visited by the butterflies were photographed and identified with a field guide of the reserve (Cornejo-Tenorio and Ibarra-Manríquez 2008). Doubtful cases were photographed in more detail and identified with other floras. Formal botanical collections were not possible due to restrictions in the reserve.

The following variables and indices were calculated with the plant data (Matteucci and Colma 1982):

- Frequency: the number of times one or more feeding plant individuals was found in the observation plots. Presence was recorded in each plot, but the three observation plots of a transect were considered a unit for analysis.
- Density: Number of plant individuals per plot.
- Cover. This refers to the proportion of the area occupied by the perpendicular projection of the aerial parts of the individuals of the species. The cover of the species was obtained by measuring the largest width of the sampled plant and using it as side length for a square. This overestimates the true cover, but as we used relative cover, it should not influence the order of relative importance adversely. From these data, the Importance Value Index was calculated with the Coefficient of Cottam and Curtis (1956), which simply adds relative frequency, relative density and relative cover. The highest possible value for this index is 300.

Later, the butterflies were counted directly during the central hours of the day (10.30–14.00). For the count, the observer stood quietly in the middle of the plot, facing north, and then counted or estimated the number of animals inserting

Fig. 2 Photos of nectaring monarch butterflies on various plant species. Photos by Nancy Sánchez-Tlacuahuac and Amancio Consuelo-Isodoro

their proboscis into the flowers. Each individual plant or 1 m^2 population (with a known number of individual plants in *Salvia*) was observed for 15s, moving clockwise. These 15-second observations were taken first for one species, then for the next. The butterfly numbers, plant species and individuals were documented with voice recording. Then, a photograph was taken of the whole plot. For each plot, the counts took about 30min; approximately 3.5h were needed for the two transects with three plots of each site. The count was interrupted if clouds or winds halted butterfly movement. The other sites were visited on different days.

Results

Plants visited for feeding and their relative importance

We observed monarch butterflies feeding on 29 species which belonged to 10 botanical families (Fig. 2). The most common family was Asteraceae with 16 species, followed

Table 1 Species visited by the monarch butterflies, their flowering season and presence of human-perceptible scent. Flowering season based on Cornejo-Tenorio and Ibarra-Manríquez (2008) and Naturalista.mx

Family	Scientific name	Seasonality	Seasonal peak	Scent
Amaryllidaceae	*Agapanthus praecox* Willd.	Mar-Jun	May	No
Asteraceae	*Ageratina areolaris* (DC.) R.M. King & H. Rob.	Aug-Feb	Nov	No
Asteraceae	*Ageratina glabrata* (DC.) R.M. King & H. Rob.	Nov-Jun	Feb	Yes
Asteraceae	*Ageratina petiolaris* (Moc. ex DC.) R.M. King & H. Rob.	Oct-Jun	Feb	No
Asteraceae	*Ageratina rivalis* (Greenm.) R.M. King & H. Rob.	Sep-Mar	Feb	No
Asteraceae	*Baccharis heterophylla* Kunth	Year-round	May	No
Asteraceae	*Barkleyanthus salicifolius* (Kunth) H. Rob. & Brettell	Jan-Jun	Mar	No
Asteraceae	*Cirsium subcoriaceum* (Less.) Sch. Bip.	Year-round	Mar	No
Asteraceae	*Packera sanguisorbae* (DC.) C. Jeffrey	Year-round	Apr	No
Asteraceae	*Roldana albonervia* Greenm.	Sep-May	Mar	No
Asteraceae	*Roldana angulifolia* (DC.) H. Rob. & Brettell	Oct-Apr	Jan	No
Asteraceae	*Senecio callosus* Sch. Bip.	Aug-Jun	Jan	No
Asteraceae	*Senecio cinerarioides* Kunth	Year-round	Mar	No
Asteraceae	*Senecio inaequidens* DC.	Year-round	Apr	No
Asteraceae	*Senecio toluccana/ Packera toluccana* (DC.) W.A. Weber & Á. Löve	Sep-Jun	Mar	No
Asteraceae	*Stevia monardifolia* Kunth	Aug-Apr	Jan	Yes
Asteraceae	*Verbesina oncophora* B.L. Rob. & Seaton	Oct-Mar	Nov	No
Fabaceae	*Lupinus montanus* Kunth	Year-round	Apr-Jul	No
Grossulariaceae	*Ribes ciliatum* Humb. & Bonpl. ex Roem. & Schult.	Oct-Mar	Mar	No
Lamiaceae	*Salvia carnea* Kunth	Sep-Apr	Dec	No
Lamiaceae	*Salvia lavanduloides* Kunth.	Year-round	Dec	No
Lamiaceae	*Salvia mexicana* L.	Jul-Mar	Oct	No
Lamiaceae	*Salvia plurispicata* Epling	Oct-May	Feb	No
Onagraceae	*Lopezia miniata* Cav.	Aug-Mar	Oct	No
Plantaginaceae	*Veronica persica* Poir.	Year-round	Feb	No
Rosaceae	*Crataegus mexicana* DC.	Year-round	Oct	No
Rosaceae	*Prunus serotina* Ehrh.	Dec-May	Mar	No
Scrophulariaceae	*Buddleja sessiliflora* Kunth	Dec-May	Feb	Yes
Solanaceae	*Solanum nigrescens* M. Martens & Galeotti	Jan-Apr	Feb	No

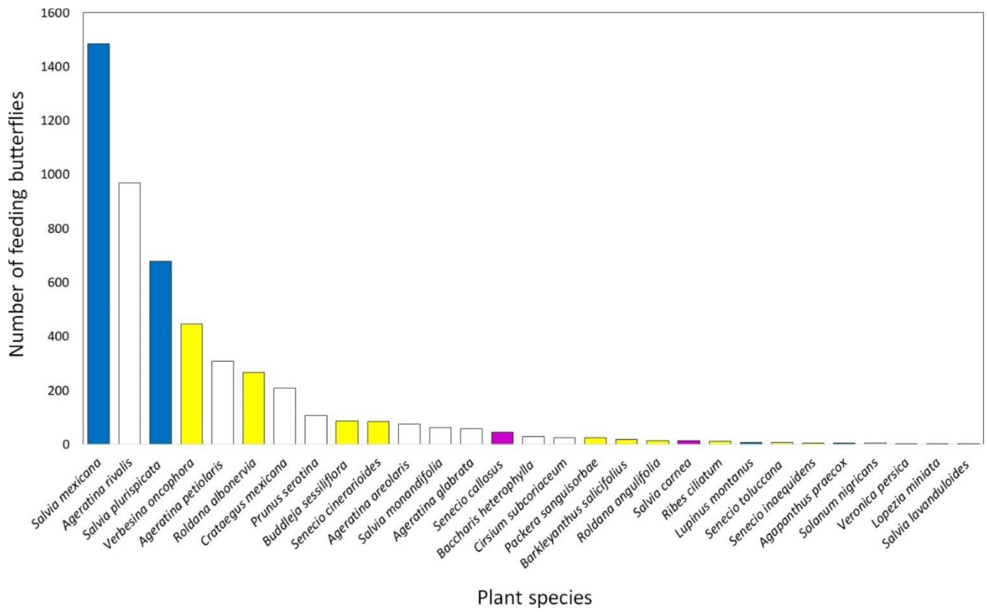
by Lamiaceae with 4 species (Table 1). Most of these species had white (10) or yellow (10) flowers, considering the spectrum of the human eye. An additional six species had blue flowers, two violet and one pink. Most species were somewhat synanthropic; some had populations within forests, but also in cultivated landscapes. Three were introduced (*Agapanthus*, *Senecio inaequidens* and *Veronica persica*). Human-perceptible scent did not appear to play a large role.

The species with most visitors were blue-flowered *Salvia mexicana* and *S. plurispicata*, as well as the white-flowered *Ageratina rivalis* (Fig. 3); however, this was related partially to their dominance in the vegetation (see Supplementary material 1). If visits per individual plant were considered (Fig. 4), two trees with white flowers (*Prunus serotina* and *Crataegus mexicana*) were in the lead, together with *Buddleja sessiliflora*; the latter has yellowish-beige flowers usually considered attractive for bees (Hinojosa-Díaz 2001). Various Asteraceae with yellow and white flowers followed.

The relative importance of the nectar-providing species in the vegetation determined frequency of butterfly nectaring (Fig. 5). The importance index had the closest relationship with the number of visits ($R^2=0.78$), with relative density a close second ($R^2=0.72$). Relative frequency and relative cover had lower values (0.65 and 0.48, respectively). However, a few species had more visitors than predicted by their importance, particularly *Ageratina rivalis* and *Verbesina oncophora*, which are weedy, attractive, winter-flowering shrubs.

Plant height did not correlate with butterfly numbers, when considering both average height per species and plant individuals (R^2 under 0.1).

Fig. 3 Number of feeding butterflies observed in all sites by species. The color of the bars represents the flower color of the species



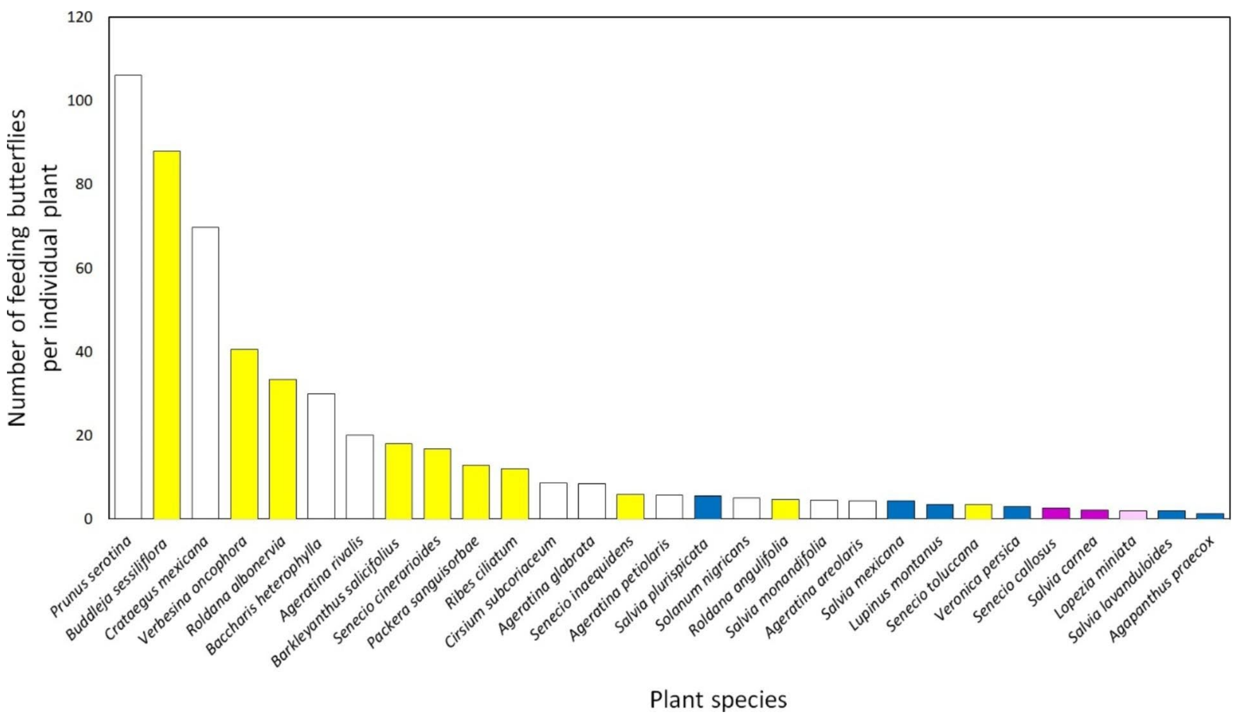


Fig. 4 Average number of feeding butterflies observed on individuals of each species (sum of the seven observation dates). The color of the bars represents the flower color of the species

Dynamics of visits and differences between transects close and farther away from colonies

During the entire period, 5020 individual feeding visits were observed (Table 2). Figure 6 shows the distribution of butterfly feeding observations of all visits. The visits to the individual sites followed a similar pattern and are not shown here.

As mentioned above, feeding visits concentrated heavily on a few groups of species, mainly composites: Eupatorieae, Senecioneae, *Verbesina*, blue-flowered *Salvia*, white-flowered Rosaceae trees and *Buddleja*. Although several other species flower at the same time, they contributed only 1.5% of the visits. Notably, the butterflies did not visit the red-colored flowers that are also abundant in the monarch fir forest, such as *Salvia elegans* Vahl. The same table

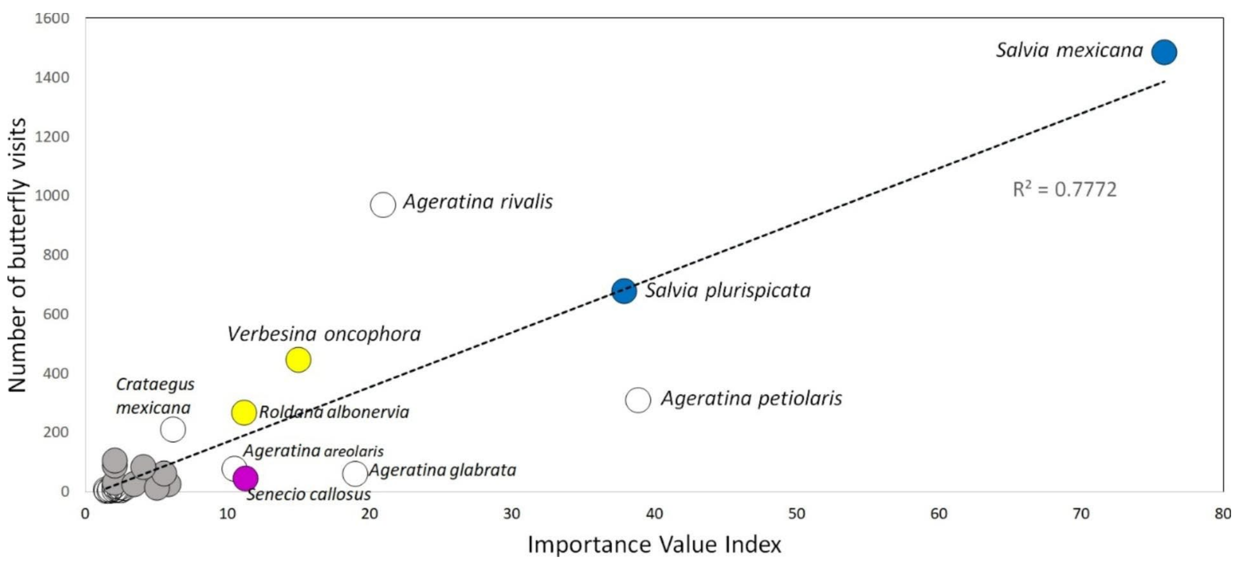


Fig. 5 Correlation between the number of butterflies and the Importance Value Index of the nectar sources

also shows considerable differences between the sites as to species; however, all conform to these groups.

There were substantial differences between the relative frequency of flowering species in the transects closer to the colonies and those farther away (Supplementary material 1). *Salvia mexicana* and *Ageratina petiolaris*, both known weedy species, were more common in the outside transects; a number of other weedier species were found only in the more disturbed places.

We observed monarchs feeding on some species not found in the observation plots. These were *Verbesina virgata, Ageratina mairetiana, Stevia subpubescens, Stevia ovata, Baccharis conferta, Senecio stoechadiformis, Salvia mocinoi, Lopezia racemosa, Clematis dioica*, and *Euphorbia pulcherrima*, the pointsettia. On waysides outside of the reserve, butterflies were particularly attracted by *Roldana albonervia* for both feeding and sunning themselves. This is a large shrub with showy yellow-flowered inflorescences in corymbiform panicles; this species was present in the study plots but uncommon and stunted.

Discussion

Monarch butterflies clearly feed in and around their winter hibernation sites, contrary to some previous statements in the literature (e.g., Masters et al. 1988). On sunny days, the "streaming" butterflies visit both water sources and flowering plants in their surroundings.

This study was not focused on the proportion of feeding butterflies or on the contribution to their nutrition, but rather on the plants visited. This feeding, particularly during the second half of the winter stay in Mexico, may support mating that initiates between mid-February and the first days of March, after the end of the reproductive diapause (Alonso-Mejia and Arellano-Guillermo 1992). These authors also noted a slight weight gain of some females towards the end of the season, though they attributed it to the addition of spermatozoids.

The visited plant species were quite similar to those the butterflies use during summer. They were dominated particularly by white and yellow-flowered composites and some Lamiaceae (e.g., Rudolph et al. 2006 in Arkansas; Tooker et al. 2002 in Illinois). The study also confirms the qualitative observations of Rendón-Salinas (1997) on the preferred genera and flower colors. Orange and yellow are preferred innately by the monarchs (Blackiston et al. 2011; these experiments did not include white). Additionally, the butterflies fed on species that are assumed to be adapted to bee-pollination, such as blue-colored salvias. These species were not the favorites, but their local abundance made them important nectar sources. Monarch butterflies are known to adapt and learn about nectar sources (Blackiston et al. 2011).

It is possible that this feeding behavior has increased due to the worsening conditions of the fir forests or of the migration routes. Thus, winter feeding may buffer deteriorating conditions of other elements of the monarchs' livelihood. Alonso-Mejía et al. (1995) expressly stated that they did not see much feeding behavior in Mexico, but it is unclear whether their observations were systematic, on sunny days, or whether they included observations outside the forests. As mentioned above, feeding butterflies were smaller and with much lower lipid reserves than those that stayed in the colonies. The decreased canopy density of the fir forests

Table 2 Nectar sources of the monarch butterflies on different dates

Plant species	Observation date (2020)							Sum
	11-Feb	**17-Feb**	**23-Feb**	**26-Feb**	**04-Mar**	**08-Mar**	**11-Mar**	
El Capulín								
Salvia mexicana	86	191	172	213	188	86	9	1179
Ageratina rivalis	92	134	90	128	112	104	9	669
Salvia plurispicata	9	22	12	10	13	8	3	77
Ageratina glabrata	3	11	12	11	10	9	3	59
Verbesina oncophora	4	11	11	8	8	5	1	48
Ageratina areolaris	2	12	9	4	6	3	0	36
Ageratina petiolaris	3	7	5	7	6	6	1	35
Senecio callosus	1	6	3	4	4	0	0	18
Cirsium subcoriaceum	3	2	1	3	3	1	0	13
Packera sanguisorbae	0	1	2	2	5	3	0	13
Salvia carnea	0	5	3	2	1	2	0	13
Senecio inaequidens	0	1	0	1	2	2	0	6
Veronica persica	1	0	1	1	0	0	0	3
Lopezia miniata	0	2	0	0	0	0	0	2
Salvia lavanduloides	0	0	1	1	0	0	0	2
Sum	224	449	383	425	404	258	30	2173
El Rosario								
	13-Feb	**19-Feb**	**25-Feb**	**28-Feb**	**06-Mar**	**10-Mar**	**13-Mar**	**Sum**
Salvia mexicana	15	58	54	87	79	8	5	306
Ageratina rivalis	33	49	38	60	58	27	2	267
Roldana albonervia	29	54	45	53	50	14	2	247
Ageratina petiolaris	31	43	38	39	37	10	3	201
Crataegus mexicana	16	40	35	25	37	30	2	185
Verbesina oncophora	16	23	28	35	28	20	2	152
Prunus serotina	16	31	24	27	3	5	0	106
Senecio cinerarioides	6	22	21	15	14	6	0	84
Salvia monandifolia	6	6	15	11	18	5	2	63
Barkleyanthus salicifolius	1	1	4	5	4	2	1	18
Baccharis heterophylla	1	5	2	3	5	1	0	17
Senecio callosus	1	4	3	3	4	1	0	16
Cirsium subcoriaceum	1	2	3	3	2	2	0	13
Packera sanguisorbae	1	1	5	2	2	2	0	13
Senecio toluccana	2	1	1	2	1	0	0	7
*Agapanthus africanus***	0	0	0	2	3	0	0	5
Solanum nigrescens	1	0	1	2	1	0	0	5
Sum	176	340	317	374	346	133	19	1705
Sierra Chincua								
	12-Feb	**18-Feb**	**24-Feb**	**27-Feb**	**05-Mar**	**09-Mar**	**12-Mar**	**Sum**
Salvia plurispicata	108	115	120	122	111	21	4	601
Verbesina oncophora	39	41	36	33	77	18	2	246
Buddleja sessiliflora	15	23	20	18	12	0	0	88
Ageratina petiolaris	15	12	14	9	16	5	1	72
Ageratina rivalis	6	11	12	14	3	2	0	48
Ageratina areolaris	3	2	12	8	9	4	2	40
Crataegus mexicana	5	2	6	3	6	2	0	24
Roldana albonervia	3	4	5	2	3	1	2	20
Roldana angulifolia	3	4	2	4	1	0	0	14
Ribes ciliatum	2	0	3	3	4	0	0	12
Senecio callosus	2	2	4	0	2	0	0	10
Lupinus montanus	1	0	1	5	0	0	0	7
Sum	202	216	235	221	244	53	11	1182

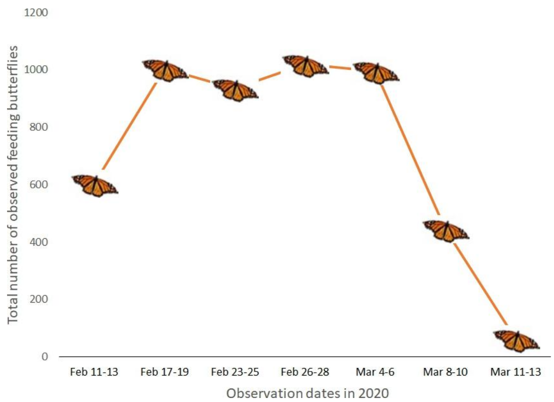


Fig. 6 Number of observed feeding butterflies in all sites

may also promote flowering plants in the understory which the stressed butterflies then visit.

Conclusion

The results point to possible interventions in support of the monarch populations: the promotion of the favorite food plants, particularly in the open areas around the Reserve. The somewhat weedy plants that could be encouraged in the agricultural areas surrounding the sanctuaries are *Ageratina petiolaris*, *A. glabrata* (which has an agreeable aroma), perhaps *A. rivalis* (though this is more of a forest plant), *Verbesina oncophora*, *Roldana albonervia*, *Prunus serotina*, *Crataegus mexicana* and the blue-colored salvias. These species would also combine pleasantly in color and size for pollinator gardens. There are likely limits to the possible support and buffer function of these plants, as they cannot substitute all other deteriorating elements of the butterflies' environment. We do not suggest further disturbance of the already stressed fir forests, but rather, promotion of a supportive landscape context.

Future investigations should focus on the relative importance of winter feeding for the monarchs. Perhaps the nectar also contributes to water uptake. A repeat study on the lipid reserve differences between perched and nectaring butterflies, including "steaming" animals, would be useful, as would studies on nectar quantity and quality of the most-visited species, and their floral ecology. More should be known about the relationship between forest cover of the perching monarchs and their nectaring behavior, the relative importance of the forest understory and the surroundings, influence of management on both microclimate and nectar sources, the energy requirements of "streaming" and of reproduction, or possible dynamics of nectaring, which may surge toward the end of their stay or be directed towards certain plants.

Supplementary Information The online version contains supplementary material available at https://doi.org/10.1007/s10841-022-00433-z.

Acknowledgements We are grateful to the ejidatarios of the Santuarios El Rosario, Sierra Chincua and El Capulín, and particularly the people of the Paradero Macheros, for their patience, interest and help in obtaining the data. The biologist Eduardo Rendón-Salinas, Ing. César Ávalos, Lic. Guadalupe Gómez, Ing. Pablo Ángeles from WWF-Mexico, and Lic. Alejandra Hinojosa from DANAIDAS helped with technical advice. Ing. Amancio Consuelo-Isidoro assisted with the fieldwork and the photographs. The work was funded by grant #868068 of Conacyt (Consejo Nacional de Ciencia y Tecnología) for the master's thesis of the first author.

Author contributions All authors developed the concept of the study and the methodology, reviewed and edited the Spanish version of the manuscript. NST did the field work, data curation, analysis and wrote the first draft. JLPE provided project administration and supervision. HV provided supervision, assisted with plant identification and wrote the English version in collaboration with NST.

Data Availability The data are available within the manuscript and in the Supplementary material.

Declarations

Declaration of competing interest The authors declare they have no conflict of interest.

References

Alonso Mejía A, Rendón Salinas E, Montesinos Patiño E (1995) Realidades energéticas de la mariposa monarca. Ciencias 39:48–49

Alonso-Mejia A, Arellano-Guillermo A (1992) Influence of temperature, surface body moisture and height aboveground on survival of monarch butterflies overwintering in Mexico. Biotropica 24:415–419

Alonso-Mejía A, Rendon-Salinas E, Montesinos-Patiño E, Brower LP (1997) Use of lipid reserves by monarch butterflies overwintering in Mexico: implications for conservation. Ecol Appl 7:934–947. https://esajournals.onlinelibrary.wiley.com/doi/10.1890/1051-0761%281997%29007%5B0934%3AUOLRBM%5D2.0.CO%3B2

Bautista Zúñiga F, Palacio Prieto JL, Delfín González H, Paéz Bistrain R (eds) (2011) Técnicas de muestreo para manejadores de recursos naturales, 2 edn. Universidad Nacional Autónoma de México, México, D.F

Blackiston D, Briscoe AD, Weiss MR (2011) Color vision and learning in the monarch butterfly, *Danaus plexippus* (Nymphalidae). J Exp Biol 214:509–520. https://doi.org/10.1242/jeb.048728

Brower LP (1995) Revisión a los mitos de Jürgen Hoth. Ciencias 39:50–51

Brower LP, Calvert WH, Hedrick LE, Cristian J (1977) Biological observations on an overwintering colony of monarch butterflies (*Danaus plexippus*, Danaidae) in Mexico. J Lepidopterists Soc 31:232–242

Brower LP, Castilleja G, Peralta A et al (2002) Quantitative changes in forest quality in a principal overwintering area of the Monarch Butterfly in Mexico, 1971–1999. Conserv Biol 16:346–359. https://doi.org/10.1046/j.1523-1739.2002.00572.x

Brower LP, Fink LS, Walford P (2006) Fueling the fall migration of the monarch butterfly. Integr Comp Biol 46:1123–1142. https://doi.org/10.1093/icb/icl029

Brower LP, Williams EH, Fink LS et al (2011) Overwintering clusters of the monarch butterfly coincide with the least hazardous vertical temperatures in the oyamel forest. J Lepidopterists' Soc 65:27–46. https://doi.org/10.18473/lepi.v65i1.a3

Brower LP, Williams EH, Jaramillo-López P et al (2017) Butterfly mortality and salvage logging from the March 2016 storm in the Monarch Butterfly Biosphere Reserve in Mexico. Am Entomol 63:151–164. https://doi.org/10.1093/ae/tmx052

Burnett V (2016) El auge del consumo de aguacate pone en peligro el hogar de las mariposas monarca en México. N. Y. Times

CONABIO (2014) Mariposa Monarca. Soy Monarca. In: Soy Monarca. https://www.soymonarca.mx/. Accessed 23 Aug 2021

Cornejo-Tenorio G, Ibarra-ManrÍquez G (2007) Plant reproductive phenology in a temperate forest of the Monarch Butterfly Biosphere Reserve, Mexico. Interciencia 32:445–452

Cornejo-Tenorio G, Ibarra-Manríquez G (2008) Flora ilustrada de la Reserva de la Biosfera Mariposa Monarca.: UNAM, Centro de Investigaciones en Ecosistemas. CONABIO, México, D.F

Cottam G, Curtis JT (1956) The use of distance measures in phytosociological sampling. Ecology 37:451–460. https://doi.org/10.2307/1930167

del Coro Arizmendi M, Nuñez Rosas LE, del Meneses Ramírez M et al (2020) Jardines para polinizadores: una herramienta para la conservacion. Universidad Nacional Autónoma de México, Ciudad de México

Díaz Barriga VH(2002) Hongos macromicetos comestibles, venenosos, medicinales y destructores de la madera, de la Reserva de la Biósfera de la Mariposa Monarca, Sierra Chincua, Michoacán, México. Fundación Produce, Michoacán, Comisión Forestal del Estado de Michoacán (COFOM), Morelia, Michoacán

Escobés R, Vignolo C (2018) Guía de los polinizadores más comunes de las zonas verdes de Madrid. Consejo Superior de Investigaciones Científicas, Madrid

Flores-Martínez JJ, Rendón-Salinas E, Martínez-Pacheco A et al (2020) Policy implementation halts deforestation in winter habitat of Monarch butterflies in Mexico. Bioscience 70:449–451. https://doi.org/10.1093/biosci/biaa038

Galindo Leal C, Salinas Rendón E (2005) Danaidas las maravillosas mariposas monarca. WWF-México, Telcel

Gutiérrez Carbonell D, Vázquez Morán VH, Trejo Monroy M et al (eds) (2001) Programa de manejo de la Reserva de la Biosfera Mariposa Monarca, México. Comisión Nacional de Áreas Naturales Protegidas, México, D. F

Hinojosa-Díaz IA(2001) Distribución altitudinal de las abejas silvestres (Hymenoptera: Apoidea) en el declive sur de la Sierra del Chichinautzin, Morelos. Master's thesis, Universidad Nacional Autónoma de México

Hobson KA, García-Rubio OR, Carrera-Treviño R et al (2020) Isotopic (δ2H) analysis of stored lipids in migratory and overwintering monarch butterflies (*Danaus plexippus*): evidence for southern critical late-stage nectaring sites? Front Ecol Evol 8:572140. https://doi.org/10.3389/fevo.2020.572140

Hoth J (1995) Mariposa monarca, mitos y otras realidades aladas. Ciencias 37:19–28

Leverkus AB, Jaramillo-López PF, Brower LP et al (2017) Mexico's logging threatens butterflies. Science 358:10081–11008. https://doi.org/10.1126/science.aar3826

Malcolm SB (1994) Milkweeds, monarch butterflies and the ecological significance of cardenolides. Chemoecology 5:101–117. https://doi.org/10.1007/BF01240595

Masters AR, Malcolm SB, Brower LP (1988) Monarch butterfly (*Danaus plexippus*) thermoregulatory behavior and adaptations for overwintering in Mexico. Ecology 69:458–467. https://doi.org/10.2307/1940444

Matteucci SD, Colma A (1982) Metodología para el estudio de la vegetación. Secretaria General de la Organización de los Estados Americanos Washington, DC, Washington, DC

Parra-Olea G, Garcia-Paris M, Papenfuss TJ, Wake DB (2005) Systematics of the *Pseudoeurycea bellii* (Caudata: Plethodontidae) species complex. Herpetologica 61:145–158. https://doi.org/10.1655/03-02

Pleasants JM, Oberhauser KS (2013) Milkweed loss in agricultural fields because of herbicide use: effect on the monarch butterfly population. Insect Conserv Divers 6:135–144. https://doi.org/10.1111/j.1752-4598.2012.00196.x

Rendón Salinas E(1997) Diagnóstico de las mariposas monarca hibernantes que intentan alimentarse y la estructura del rodal del bosque donde se agrupó la colonia del Llano del Toro en la Sierra Chincua, Mich., durante la temporada de hibernación 1993–1994. Undergraduate thesis, Universidad Nacional Autónoma de México

Rendón-Salinas E, Martínez-Meza F, Mendoza-Pérez MA et al(2019) Superficie forestal ocupada por las colonias de mariposas Monarca en México durante la hibernación de 2018–2019. WWF-México. Unpublished report., Ciudad de México

Rendón-Salinas E, Martínez-Meza F, Mendoza-Pérez MA et al(2020) Superficie forestal ocupada por las colonias de mariposas Monarca en México durante la hibernación de 2019–2020. WWF-México. Unpublished report., Ciudad de México

Rendón-Salinas E, Martínez-Meza F, Mendoza-Pérez MA et al(2021) Superficie forestal ocupada por las colonias de mariposas Monarca en México durante la hibernación de 2020–2021. WWF-México. Unpublished report., Ciudad de México

Rendón-Salinas E, Pérez-Ojeda J, Ibarra-Contreras A, Galindo-Leal C (eds) (2005) Primer foro regional mariposa monarca. Memorias. Valle de Bravo, Estado de México

Rogel-Fajardo I, Rojas-Lopez A, Ortega-Vega SY (2011) El turismo alternativo como estrategia de conservación de la reserva de la biosfera de la mariposa monarca (2008–2010). Quivera Rev Estud Territ 13:115–133

Rudolph DC, Ely CA, Schaefer RR et al (2006) Monarch (*Danaus plexippus* L. Nymphalidae) migration, nectar resources and fire regimes in the Ouachita Mountains of Arkansas. J Lepidopterists Soc 60:165–170

Rzedowski J(2006) Vegetación de México. Primera edición digital. Comisión Nacional para el Conocimiento y Uso de la Biodiversidad, México, D. F

SEMARNAT CONANP(2018) Plan de Acción para la Conservación de la Mariposa Monarca en México, 2018/2024. 1a ed. Secretaría de Medio Ambiente y Recursos Naturales y Comisión Nacional de Áreas Naturales Protegidas, Ciudad de México

SEMARNAT/INECC (1996) Reserva Especial de la Biosfera Mariposa Monarca. Instituto Nacional de Ecología y Cambio Climático. Secretaría de Medio Ambiente y Recursos Naturales, México, D. F

Tamayo JL(1962) Geografía general de México. Instituto Mexicano de Investigaciones Económicas, México, D. F

Tooker JF, Reagel PF, Hanks LM (2002) Nectar sources of day-flying Lepidoptera of central Illinois. Ann Entomol Soc Am 95:84–96. https://www.bioone.org/doi/pdf/10.1603/0013-8746(2002)095%5B0084:NSODFL%5D2.0.CO%3B2

Vidal O, López-García J, Rendón Salinas E (2014) Trends in deforestation and forest degradation after a decade of monitoring in the Monarch Butterfly Biosphere Reserve in Mexico. Conserv Biol 28:177–186. https://doi.org/10.1111/cobi.12138

WWF-México (2020) Degradación forestal en la Zona Núcleo de la Reserva de la Biosfera Mariposa Monarca 2019–2020. WWF-México. Unpublished report., Ciudad de México