



**Cover photo and photo above.** A group of monarch butterflies (*Danaus plexippus*) covers an oyamel fir tree (*Abies religiosa*) at an overwintering site in the Piedra Herrada Monarch Butterfly Sanctuary in Mexico. Cover photograph by Steven B. Hilburger, U.S. Geological Survey.

# Summary of Available Data from the Monarch Overwintering Colonies in Central Mexico, 1976–1991

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Prepared in cooperation with the U.S. Fish and Wildlife Service	
Open-File Report 2020–1150	

### U.S. Geological Survey, Reston, Virginia: 2021

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#### Suggested citation:

Zylstra, E.R., Thogmartin, W.E., Ramírez, M.I., and Zipkin, E.F., 2020, Summary of available data from the monarch overwintering colonies in central Mexico, 1976–1991: U.S. Geological Survey Open-File Report 2020–1150, 10 p., https://doi.org/10.3133/ofr20201150.

ISSN 2331-1258 (online)

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Monarch with worn wings. Photograph by Steven B. Hilburger, U.S. Geological Survey.

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#### **Overview**

Historical estimates of the area occupied by overwintering *Danaus plexippus* (monarchs) in central Mexico (between winters of 1976 and 1991) were published in García-Serrano and others (2004) and more recently in Mawdsley and others (2020). Our primary objectives were to identify the specific data that informed those estimates and, importantly, determine the degree to which the reported estimates reflect the total size of the overwintering monarch population during that period. Understanding how historical estimates of the overwintering area relate to total population size is necessary to ensure that inferences about population abundance and temporal trends are reliable, particularly as the U.S. Fish and Wildlife Service is in the process of determining if the species should be listed under the U.S. Endangered Species Act.

### Monarch Migratory Cycle and Overwintering Ecology

Each year, monarchs east of the Rocky Mountains in North America migrate thousands of kilometers through multiple generations (Brower, 1995). In early spring, monarchs leave their overwintering sites in central Mexico and migrate to breeding grounds in the southern United States to produce the first generation of the year. That first generation then migrates to summer breeding grounds in the northern United States and southern Canada, where two to three more generations are produced. Starting in late summer and early autumn, individuals in the final generation enter reproductive diapause and migrate south to the same overwintering sites in central Mexico. Thus, individuals present on the overwintering grounds in one year are three to four generations removed from individuals present the year before (Oberhauser and others, 2017).

Monarchs spend the winter in high-elevation forests, primarily aggregating in stands of *Abies religiosa* (oyamel fir) that grow along the Transvolcanic Belt in the Mexican states of Michoacán and México (Vidal and Rendón-Salinas, 2014). These dense, mature forest stands protect monarchs from extreme temperatures and precipitation and allow them to survive and remain in reproductive diapause throughout the winter (Williams and Brower, 2015).

Monarchs begin arriving on the overwintering grounds in late October/early November (Calvert and Brower, 1986). Shortly after arrival, monarchs are relatively active, forming numerous smaller aggregations. After this initial settlement period, monarch activity slows and by December, smaller aggregations coalesce into well-defined, densely packed aggregations (often referred to as colonies). Monarch activity increases as temperatures rise in February and early March. During this period, the colonies spread out—increasing the area covered and decreasing density, and shift downslope as individuals make daily foraging trips to water sources. Monarchs begin leaving the overwintering grounds in March, migrating north to produce the first generation of the year on the spring breeding grounds in the southern U.S. (Calvert and Brower, 1986).

### Data Collection at Overwintering Colonies, 1993–2019

In each winter since 1993–1994 (hereafter we refer to winter seasons by the year associated with December, here 1993), researchers surveyed all locations where monarchs were currently or historically known to overwinter. Colonies were assigned names based on the agrarian, State, Federal, or private property in which the colony was located (Vidal and Rendón-Salinas, 2014; table 1). Only a subset of properties is occupied each year, and the geographic location of a colony within a property, when present, varies over time.

To estimate population size, researchers delineated the perimeter of each colony and estimated the area occupied, in hectares, in the second half of December. The sum of these

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Table 1. Overwintering monarch colonies in central Mexico that were surveyed between 2004 and 2019. We combined colonies that were in close proximity to each other to create supercolonies because it was not possible to associate historical measurements with individual colonies. % total area occupied is the mean percent of the overwintering population (in other words, total area occupied) associated with each supercolony between 2004 and 2019 (in other words, the proportional contribution of each supercolony to the overwintering population between 2004 and 2019), along with the range of annual values. We also list the names (Calvert and Brower, 1986) or specific locations (Mejía, 1996) of monarch aggregations provided in the original data sources. We did not include two colonies outside of the Monarch Butterfly Biosphere Reserve that were only surveyed in 2018–2019.

[MBBR, Monarch Butterfly Biosphere Reserve; %, percent; –, not applicable]

MBBR reserve	Sanctuary	Supercolony	Colony	% total area occupied, 2004–2019 (range)	Names of aggregations, Calvert and Browera	Names of aggregations/ localities, Mejía
Inside	Cerro Pelón	Cerro Pelón W	El Capulin San Juan Xoconusco Nicolas Romero	13.4 (0, 33.8)	Pelon	Carditos, Cerro la Cuchilla del Cajón, El Terrero, Gota de Agua, La Cueva, Llano Tres Gobernadores, Loma Larga
Inside	Cerro Pelón	Cerro Pelón E	MA de Xoconusco SP Malacatepec	5.8 (0, 25.4)	-	-
Inside	Sierra Campanario	La Mesa	La Mesa	2.2 (0, 9.2)	Picacho	_
Inside	Sierra Campanario	El Rosario	El Rosario	41.3 (20.8, 77.6)	Campanario	Balsitas, El Sendero Las Palmas, Llano Cruzado, Llano de los Conejos, Los Horcones, Los Letreros
Inside	Cerro Altamirano	Contepec	Contepec	0.1 (0, 1.4)	Altamirano	Cañada de las Cruces
Inside	Chivati-Huacal	Carpinteros	Carpinteros	3.0 (0, 15.1)	Chivati	Cerro Chivati, Llano de los Toros (Huacal)
Inside	Sierra Chincua	Sierra Chincua	Propiedad Federal Propiedad Estatal Cerro Prieto El Calabozo Fraccion	13.4 (3.0, 31.4)	Chincua	Barranca Honda, El Mirador, Llano del Toro, Peña Cargada, Zapateros
Inside	Lomas de Aparicio	Crescencio Morales	Crescencio Morales	0.9 (0, 7.8)	-	_
Outside	Cerro del Amparo	San Francisco Oxtotilpan	SF Oxtotilpan	1.9 (0, 4.6)	=	=
Outside	Palomas	San Antonio Albarranes	SA Albarranes	8.3 (1.2, 27.4)	_	-
Outside	Piedra Herrada	San Mateo Almomoloa	a SM Almomoloa 5.5 (2.9, 10.1) Herrada		-	
Outside	Los Azufres	San Andrés	San Andrés	2.1 (0, 6.7)	San Andres	-
Outside	Mil Cumbres	Río de Parras	Río de Parras	1.9 (0, 7.0)	-	_

aWhen multiple aggregations were measured in the same supercolony/sanctuary, Calvert and Brower (1986) assigned numbers to each aggregation name (for example, Chincua 1, Chincua 2).

areas is used as an annual index of population size (García-Serrano and others, 2004; Vidal and Rendón-Salinas 2014). Translating estimates of area occupied to estimates of abundance requires knowledge about the density of individuals in a three-dimensional landscape (Thogmartin and others, 2017). However, monarch densities within colonies are highly uncertain and vary over the course of winter with dew point and temperature (Calvert, 2004; Brower and others, 2011). Therefore, we used estimates of the area occupied as an index of population size, as previous studies have done.

Between 1993 and 2003, observers from Comisión Nacional de Áreas Naturales Protegidas (CONANP) and the Monarch Butterfly Biosphere Reserve (MBBR) led data collection efforts, reporting annual estimates of the total area occupied across all colonies. The World Wildlife Fund-Mexico (WWF) in alliance with CONANP began leading data collection efforts starting in December 2004, reporting estimates of the area occupied by monarchs in each colony instead of a single aggregate value. A total of 21 colonies have been surveyed by WWF since 2004, 19 of which were surveyed in all years (2 colonies were first located and surveyed in winter 2018–2019; table 1). Most colonies are located within the MBBR, which was established in 2000 to protect forests inhabited by the overwintering population (Missrie, 2004).

For the purposes of this report, we combined late-December estimates of the area occupied among colonies that were in close proximity to one another and refer to these units as "supercolonies" (n = 13; table 1). We used estimates from supercolonies rather than colonies because it was difficult to associate historical measurements with individual colonies when the locations of several colonies were near one another, occasionally shifted within or among seasons, and intersected property boundaries.

### Historical Data, 1976–1990

There are two primary sources of data on monarch overwintering colonies in central Mexico before 1993: Calvert and Brower (1986) reported the area occupied by aggregations of monarchs between 1976 and 1981 and Mejía (1996) reported the area occupied by aggregations of monarchs between 1984 and 1990<sup>1</sup>. These early studies focused primarily on describing the size, locations, and phenology of overwintering aggregations in five sanctuaries where monarchs were known to gather: Cerro Pelón, Sierra Campanario, Cerro Altamirano, Chivati-Huacal, and Sierra Chincua (tables 1 and 2; García-Serrano and others 2004). Less effort was expended to locate monarch aggregations that formed outside of these sanctuaries.

We were able to link aggregations described in Calvert and Brower (1986) and Mejía (1996) to supercolonies using (1) the name of the sanctuary, municipality, property, or specific location associated with each aggregation and (2) the geographic location (latitude/longitude) of the aggregation, when provided. On numerous occasions, Calvert and Brower (1986) and Mejía (1996) measured multiple monarch aggregations in close proximity to each other that were associated with the same supercolony. In addition, aggregations were often measured multiple times in a winter season, with some measured as early as 4 November and some as late as 30 March.

For each supercolony and season, we used two criteria to select measurements on which to base our inferences. We selected one measurement per season for each aggregation with the goal of (1) minimizing the duration of time between measurements of different aggregations within a supercolony and (2) selecting measurements that were made during, or as near as possible to, the second half of December (43 percent of selected measurements took place in December; 76 percent of selected measurements took place between 27 November and 31 January, when monarchs are less active and aggregations are relatively stable; table 2).

<sup>&</sup>lt;sup>1</sup>E. R. Zylstra extracted data from Calvert and Brower (1986), and M. I. Ramírez extracted data from Mejía (1996).

**Table 2.** Numbers of aggregations and dates of measurements used to estimate the total area occupied (hectare) in central Mexico by monarchs in each supercolony and winter season. Year listed is that associated with December in a given winter season (for example, 1976 represents the 1976–1977 winter season).

[ha, hectare; CB, Calvert and Brower (1986);m/d/yyyy, date written as month/day/year; M, Mejía (1996)]

	Data			Number of		Measure	ement date(s)
Year	source	Supercolony	Aggregation/location name(s)	aggregations	Total area (ha)	Earliest	Latest
1976	СВ	Sierra Chincua	Chincua 1	1	1.50	1/27/1977	1/27/1977
1977	CB	Cerro Pelón W	Pelon	1	1.47	1/31/1978	1/31/1978
1977	CB	Sierra Chincua	Chincua 1, Chincua 2	2	3.38	2/2/1978	2/16/1978
1977	CB	Contepec	Altamirano	1	0.69	11/27/1977	11/27/1977
1977	CB	SM Almomoloa	Herrada	1	0.25	1/24/1978	1/24/1978
1978	CB	Sierra Chincua	Chincua 1, Chincua 4a	2	4.78	12/6/1978	12/13/1978
1978	CB	Contepec	Altamirano	1	0.19	12/14/1978	12/14/1978
1979	CB	Sierra Chincua	Chincua 1, Chincua 2, Chincua 3, Chincua 4	4	1.32	1/6/1980	1/18/1980
1979	CB	San Andrés	San Andres	1	0.19	12/3/1979	12/3/1979
1980	CB	Sierra Chincua	Chincua 6, Chincua 7 <sup>b</sup>	2	3.16	1/8/1981	1/11/1981
1981	CB	Carpinteros	Chivati	1	0.20	3/7/1982	3/7/1982
1981	CB	Sierra Chincua	Chincua	1	1.47	2/8/1982	2/8/1982
1981	CB	La Mesa	Picacho 1	1	2.03	3/6/1982	3/6/1982
1981	CB	El Rosario	Campanario	1	3.34	3/6/1982	3/6/1982
1984	M	Carpinteros	Llano de los Toros (Huacal)	1	0.40	1/5/1985	1/5/1985
1984	M	Cerro Pelón W	La Cueva	1	0.56	1/31/1985	1/31/1985
1984	M	Sierra Chincua	Barranca Honda	1	0.51	1/9/1985	1/9/1985
1984	M	El Rosario	El Sendero	1	1.67	1/25/1985	1/25/1985
1985	M	Carpinteros	Cerro Chivati	1	0.18	1/3/1986	1/3/1986
1985	M	Cerro Pelón W	Loma Larga	1	2.36	12/5/1985	12/5/1985
1985	M	Sierra Chincua	Llano del Toro, Peña Cargada	2	2.69	12/6/1985	12/6/1985
1985	M	Contepec	(Unspecified)	1	0.01	2/2/1986	2/2/1986
1985	M	El Rosario	Los Horcones	1	3.18	12/13/1985	12/13/1985
1986	M	Sierra Chincua	Barranca Honda, Peña Cargada	2	1.20	1/15/1987	2/27/1987
1986	M	El Rosario	El Sendero	1	1.15	1/14/1987	1/14/1987
1987	M	Cerro Pelón W	Cerro la Cuchilla del Cajón, El Terrero	2	2.68	12/21/1987	12/21/1987
1987	M	Sierra Chincua	Barranca Honda, Peña Cargada	2	1.45	12/10/1987	3/11/1988
1987	M	El Rosario	El Sendero	1	1.53	12/16/1987	12/16/1987
1988	M	Sierra Chincua	Barranca Honda, El Mirador, Llano del Toro	3	8.46	12/18/1988	3/30/1989

Historical Data, 1976–1990

**Table 2.** Numbers of aggregations and dates of measurements used to estimate the total area occupied (hectare) in central Mexico by monarchs in each supercolony and winter season. Year listed is that associated with December in a given winter season (for example, 1976 represents the 1976–1977 winter season).—Continued

[ha, hectare; CB, Calvert and Brower (1986);m/d/yyyy, date written as month/day/year; M, Mejía (1996)]

V	Data	Company	A	Number of	Total area	Measurement date(s)		
Year	source	Supercolony	Aggregation/location name(s)	aggregations	(ha)	Earliest	Latest	
1988	M	El Rosario	El Sendero, Los Letreros	2	5.69	12/22/1988	2/24/1989	
1989	M	Cerro Pelón W	Carditos	1	0.33	12/28/1989	12/28/1989	
1989	M	Sierra Chincua	Llano del Toro	1	3.46	12/13/1989	12/13/1989	
1989	M	El Rosario	Las Palmas, Llano Cruzado, Los Horcones, Los Letreros	4	5.73	12/11/1989	12/12/1989	
1990	M	Cerro Pelón W	Gota de Agua, Llano Tres Gobernadores	2	1.50	12/29/1990	1/28/1991	
1990	M	Sierra Chincua	Llano del Toro, Zapateros	2	10.34	12/21/1990	2/25/1991	
1990	M	Contepec	Cañada de las Cruces	1	0.30	2/20/1991	2/20/1991	
1990	M	El Rosario	Bassitas, El Sendero, Llano de los Conejos, Los Letreros	4	6.22	12/19/1990	1/27/1991	

<sup>&</sup>lt;sup>a</sup>Calvert and Brower (1986) measured six aggregations in the Chincua supercolony in 1978 but noted that four of the aggregations (Chincua 2, 3, 5, and 6) merged with Chincua 4 by late December or early January.

bCalvert and Brower (1986) measured seven aggregations in the Chincua supercolony in 1980, but five of these aggregations (Chincua 1–5) merged to form Chincua 7 by early January.

### Inferences About Monarch Population Size and Trends

Between 1976 and 1990, 0-5 supercolonies were surveyed each year (table 3). Supercolonies surveyed before 1993 were among the largest colonies in the overwintering population between 2004 and 2019 (table 3), and most were included in the MBBR when it was established in 2000 (table 1). Assuming that the proportional contribution of each supercolony to overwintering populations between 1976 and 1990 was the same as that observed between 2004 and 2019 suggests that only 13-60 percent of the overwintering population was surveyed annually between 1976 and 1981 and 55-71 percent of the overwintering population was surveyed annually between 1984 and 1990 (table 3). This assumption implies that measurements of the total area occupied across surveyed supercolonies (that is, 1976-1990 values reported in García-Serrano and others, 2004 and Mawdsley and others, 2020) are likely vast underestimates of the area occupied by the entire overwintering monarch population, particularly in 1976–1981 (fig. 1). Combining historical measurements of the area occupied (which are based on surveys at a few number of locations) with measurements from recent years (which are based on annual surveys at all historical locations) will bias inferences about population trends, as this implicitly assumes that monarchs were absent from locations when they were not surveyed; that is, estimates of population trend based on historical values that do not account for survey effort (for example, trend estimates in Mawdsley and others [2020]) will underestimate true declines in the overwintering population.

There are reasons to be cautious when making inferences about population size or temporal trends in the overwintering monarch population based on historical data. Such inferences depend on multiple strong assumptions including that (1) observers reported all survey effort, even if monarchs were absent<sup>2</sup>; (2) observers found and measured all aggregations within a supercolony when it was surveyed; (3) methods used to measure the area occupied were consistent over time or, if different, did not result in systematic bias; (4) monarch densities were constant over time and among aggregations; (5) monarchs in the overwintering population were distributed among supercolonies in the same way each year; and (6) there were no changes over time in the amount of habitat available to overwintering monarchs. Clearly, some of these assumptions are more tenable than others.

Therefore, instead of estimating trends in the overwintering population based on extrapolated estimates of population size between 1976 and 1990 (fig. 1), we evaluated trends for several supercolonies that comprise a large part of overwintering population in recent years and were surveyed on multiple occasions between 1976 and 1990. Assuming that the relative contribution of these supercolonies has been constant over time, negative trends in the area occupied by these supercolonies would indicate declines in the overwintering monarch population. Despite infrequent surveys, there were negative trends in each of the three supercolonies we were able to evaluate (fig. 2), providing further evidence that the eastern monarch population has declined since studies began in the mid-1970s.

<sup>2</sup>Calvert and Brower (1986) reported two aggregations that occupied zero hectares late in the winter season, indicating that this assumption may be reasonable.



Monarch male in the sun. Photograph by Steven B. Hilburger, U.S. Geological Survey

**Table 3.** Summary of survey efforts and measurements of area occupied by overwintering monarch aggregations in central Mexico between 1976 and 1990 (years associated with December in each winter season; for example, 1976 represents the 1976–1977 winter season). Values represent the estimated area occupied (in hectares) by all monarch aggregations associated with a given supercolony. Estimates for 1976–1981 were provided by Calvert and Brower (1986) and estimates for 1984–1990 were provided by Mejía (1996). No surveys were completed in 1982–1983. Percent of population surveyed is an estimate of the percent of the overwintering monarch population sampled each year, assuming that monarchs were distributed among supercolonies similar to how they were distributed between 2004 and 2019 (see table 1).

[ha, hectare; –, not applicable]

Construent	Cunavaalamu	Calvert and Brower (1986) <sup>1</sup>					<b>M</b> ejía (1996)¹							
Sanctuary	Supercolony	1976	1977	1978	1979	1980	1981	1984	1985	1986	1987	1988	1989	1990
Cerro Pelón	Cerro Pelón W	-	1.47	-	-	-	_	0.56	2.36	_	2.68	_	0.33	1.50
Cerro Pelón	Cerro Pelón E	-	-	_	_	_	_	_	-	-	-	_	-	-
Sierra Campanario	La Mesa	-	-	-	-	-	2.03	_	-	-	-	-	-	-
Sierra Campanario	El Rosario	-	-	_	_	_	3.34	1.67	3.18	1.15	1.53	5.69	5.73	6.22
Cerro Altamirano	Contepec	-	0.69	0.19	-	-	_	_	0.01	-	-	-	-	0.30
Chivati-Huacal	Carpinteros		-	_	_	_	0.20	0.40	0.18	-	-	_	-	-
Sierra Chincua	Sierra Chincua	1.50	3.38	4.78	1.32	3.16	1.47	0.51	2.69	1.20	1.45	8.46	3.46	10.34
Lomas de Aparicio	Crescencio Morales		-	_	_	_	_	_	_	-	-	_	-	-
Cerro del Amparo	San Francisco Oxtotilpan	-	-	-	-	-	_	_	-	-	-	-	-	-
Palomas	San Antonio Albarranes		-	_	_	_	_	_	_	-	-	_	-	-
Piedra Herrada	San Mateo Almomoloa	-	0.25	-	-	-	_	_	-	-	-	-	-	-
Los Azufres	San Andrés		-	_	0.19	_	_	_	_	-	_	_	-	-
Mil Cumbres	Río de Parras	-	-	-	-	-	_	_	-	-	-	-	-	-
Total area measured (ha)		1.50	5.79	4.97	1.51	3.16	7.04	3.14	8.42	2.35	5.66	14.15	9.52	18.36
Number of supercolonies surveyed		1	4	2	2	1	4	4	5	2	3	2	3	4
Percent of population surveyed		13	32	14	16	13	60	71	71	54	68	55	68	68

<sup>&</sup>lt;sup>1</sup>E. R. Zylstra extracted data from Calvert and Brower (1986), and M. I. Ramírez extracted data from Mejía (1996).

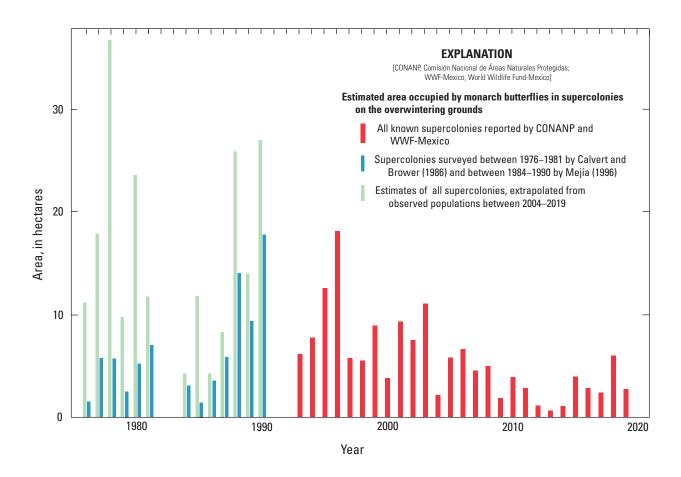


Figure 1. Estimated area occupied (hectare) by monarch butterflies on the overwintering grounds in central Mexico. The red bars represent estimates of the total area occupied across all known supercolonies reported by Comisión Nacional de Áreas Naturales Protegidas and World Wildlife Fund Mexico. The blue bars are based on Figure 1 in Mawdsley and others (2020) and represent the area occupied by monarch butterflies in supercolonies that were surveyed between 1976–1981 by Calvert and Brower (1986) and surveyed between 1984–1990 by Mejía (1996). The light green bars represent estimates of the total area occupied by monarch butterflies across all supercolonies, assuming that the proportional contribution of each supercolony to the entire overwintering population was the same as that observed between 2004–2019. We provide these extrapolated estimates of population size between 1976–1990 to illustrate that the values presented in Mawdsley and others (2020), which do not account for survey effort, are unlikely to represent the size of the entire eastern migratory population during this period. We do not estimate trend in the monarch population between 1976–2019 using the extrapolated 1976–1990 estimates because these estimates do not have associated measures of uncertainty and rely on assumptions that cannot be independently verified.

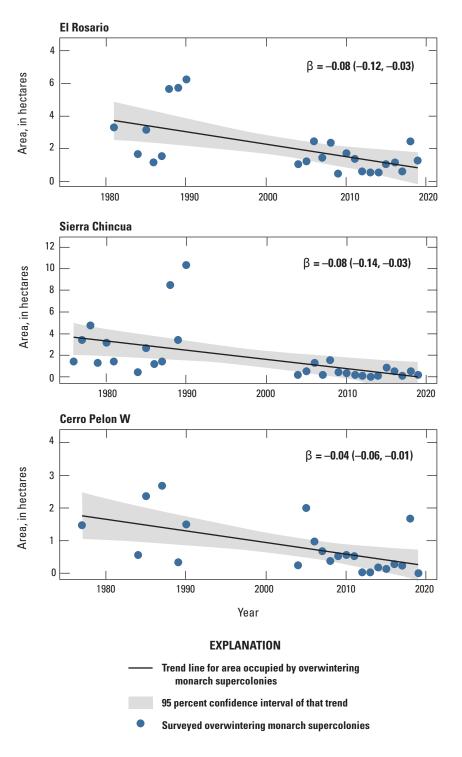


Figure 2. Area occupied (hectare) in three overwintering supercolonies in central Mexico that were surveyed prior to 1993. On average, 41 percent, 13 percent, and 13 percent of annual overwintering populations between 2004 and 2019 were associated with El Rosario, Sierra Chincua, and Cerro Pelon W supercolonies, respectively. Black lines and shaded areas represent linear trends with 95 percent confidence intervals (estimated slopes, with 95 percent confidence intervals, provided at the top right of each panel).

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Publishing support provided by the Indianapolis Publishing Service Center