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OVERWINTERING AREAS AND MIGRATORY ROUTES OF THE MONARCH BUTTERFLY (*DANAUS P. PLEXIPPUS*, LEPIDOPTERA: DANAIDAE) IN NORTH AMERICA, WITH SPECIAL REFERENCE TO THE WESTERN POPULATION

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Abstract *Can. Ent.* 109: 1583–1589 (1977)

As a result of alar tagging migrating specimens of the monarch butterfly (*Danaus p. plexippus* L.) in North America over a period of 25 years, it was possible to plot the migration routes establishing two large overwintering colonies, one located in California and the other in mountains of the Sierra Madre Occidentale in Mexico. Photographs of the two overwintering populations are presented together with release–recapture lines showing the direction of migration from breeding areas to the two overwintering sites. Data, presented for the first time, show the migration routes of the Western population from the breeding areas in the mountains and west of the mountains to California.

Introduction

When we first started our investigations of the migrations of the monarch butterfly in 1937, it had been suggested, in published reports, that the monarch butterflies from the eastern portions of North America overwintered in Florida (Williams 1930). However, large overwintering colonies were known to occur in California (Fig. 3) and so it was further suggested that perhaps migrants from the eastern parts of the continent travelled westward eventually arriving at the Pacific coast of California. There were, therefore, two primary questions to be answered: Where did the monarch butterflies from eastern North America overwinter? What breeding grounds produced the monarch butterflies that overwintered in California?

Data concerning the origin of the Californian overwintering populations are here presented for the first time as a result of more than 20 years of investigations.

For comparative purposes, summary data for the eastern populations from previous published reports have been included.

Summary of Methods Used

The primary method used to follow the movements of the migrating monarchs was that of the alar tag system now in use in many parts of the world and initiated in our research in 1937. This consists of placing an adhesive identifying label, bearing a specific number and a return address, on the leading edge of the right front wing of the migrant (Urquhart 1941, 1960, 1976; Urquhart and Urquhart 1976*a*, 1976*b*).

An Insect Migration Association was established in 1952 for the purpose of tagging the butterflies in various parts of the continent and recording data on numbers, presence of larvae, food plant, and weather. From 1952 to 1976 more than 3000 volunteers took part in the program.

Expeditions to various parts of the continent—through southern Canada, central and southern United States of America, Mexico, and Central America—for an accumulated distance of over 152,000 miles were made to obtain distributional records in various stages of development and to obtain specimens of the larval food plant. In the course of these travels, 38 universities and colleges were visited to examine research collections and discuss problems relating to the research with staff biologists.

In areas where monarch butterflies were scarce, and hence relatively few specimens could be alar-tagged, a method of specimen transfer was initiated whereby migrants from areas of great abundance were sent by airmail to be released in areas of relative scarcity such as Gibsons, British Columbia; Salem, Oregon; and Reno, Nevada (Table I).

Table I. Release and recapture of alar-tagged specimens during the autumnal migration for the plains and western regions—eastern data (Urquhart 1960)

Alar-tagged at	Recaptured at	Direction flown		Distance (km)
	Plains Region			
Towner, North Dakota	Omaha, Nebraska	SSE	(161)	885
	Dwight, Kansas	SSE	(166)	1167
	Pratt, Kansas	S	(180)	1215
	Western Regions			
Gibsons, British Columbia	Seattle, Washington	SSE	(154)	235
	Central Point, Oregon	S	(176)	837
	Bolina, California	S	(174)	1360
Salem, Oregon	Reedsport, Oregon	SSW	(200)	169
	Port Orford, Oregon	SSW	(206)	277
	Gold Beach, Oregon	SW	(225)	324
	Smith River, Oregon	SSW	(192)	367
	San Rafael, Oregon	S	(176)	806
	Muir Beach, California	S	(178)	845
	Bolinas, California	S	(178)	853
Boise, Idaho	Carmel, California	SSW	(209)	982
	Arroyo Grande, California	SSW	(201)	1046
	Morro Bay, California	SSW	(204)	1046
	Ventura, California	SSW	(192)	1102
Reno, Nevada	New Brighton State State Beach, California	SSW	(215)	362
	Morro Bay, California	SSW	(192)	459
	Pismo Beach, California	SSW	(190)	507
Santa Cruz, California	Marina, California	SE	(127)	29
	Aromas, California	SE	(112)	34
	Carmel, California	S	(170)	48
	Coalinga, California	SE	(122)	177
	Grover City, California	SSE	(147)	282
Whittier, California	Carlsbad, California	SE	(140)	121
	Leucadia, California	SSE	(148)	129
	Del Mar, California	SSE	(149)	145
	La Jolla, California	SSE	(148)	161

The success of the program was enhanced by publicity. When a tagged specimen was recaptured the person finding it often referred it to the local newspaper thus alerting the general public and making it possible for more alar-tagged specimens to be returned to our laboratory.

Results

On 9 January 1975, as a result of plotting the movements of the alar-tagged specimens from the return of tagged specimens, the overwintering site of the eastern population of the monarch butterfly was finally discovered on the slopes of volcanic mountains in the Sierra Madre Occidentale in south-central Mexico (Fig. 4) (Urquhart 1976; Urquhart and Urquhart 1976*a*). That this was unquestionably the overwintering site of the eastern population was confirmed by the recapture of specimens from various parts of the United States of America east of the Rocky Mountains (Urquhart 1976; Urquhart and Urquhart 1976*a*).

Observations and collections of the various stages during 1937–39 and 1952–76 have indicated the breeding areas of the western population (Fig. 1).

Recapture of migrants tagged in the Rocky Mountains and areas west of the mountains has established the origin of colonies overwintering in California (Figs. 3, 2).

General Discussion

The remarkable ability of the monarch butterfly to travel such great distances is due to the physiological state of reproductive dormancy together with the presence of large amounts of stored fat which prolongs the life span to 9 months or more (Urquhart and Stegner 1966). As a result the monarch butterfly has a very wide distribution extending from the North American continent to various other continents and islands of the world (Urquhart 1960). During the southward migration the food requirement is obtained from various species of nectar-producing flowers and, apparently, the fat reserve is not utilized. During the vernal migration from the overwintering sites, the fat reserve is made available at a time when very few nectar-producing plants are available. Two explanations accounting for the inertness of the stored fat and its later availability have been offered by biochemistry colleagues. One suggestion is that the enzyme lipase is secreted after the overwintering period but not before; and the other that there may be a change from a saturated to an unsaturated fat. Whatever the biochemical and physiological mechanisms may be, the evolution of the fat storage system has made it possible for this particular insect to behave like a migrating bird, the one exception being that the journey to the overwintering grounds and back is made only once. Hence, each year a new generation migrates from breeding to overwintering grounds.

FIG. 1. Eastern (•) and western (▪) population distribution based on specimens collected at the sites indicated. Many hundreds of localities are recorded for the eastern population of which only a few representatives have been plotted for comparative purposes.

In addition to migratory populations that occur towards the end of the summer period, resulting from decreasing light period and lower temperatures, there are, in various areas, populations that do not appear to migrate. These have been termed "resident populations" (Urquhart *et al*. 1968). These non-migrating populations occur in those geographic areas where the temperature remains relatively high (temperatures below 0° C being of rare occurrence and short duration) and the larval food plant is available. This combination occurs in southern California, southern Mexico, and Central America. These continual breeding populations are similar to laboratory populations where the temperature remains constant and the daylight period is prolonged by artificial illumination (Urquhart and Stegner 1966). Whether or not such non-migrants can, under certain climatic conditions, become migrants is not known,

FIG. 2. Release–recapture lines showing migration routes to the overwintering sites. A, western population; B, eastern population; C, area of maximum breeding population of the eastern population; D, aberrant migration route of the eastern population through Peninsular Florida to Cuba; E, suggested aberrant migration to Yucatan; F, scattered, free-flying individuals recorded in southern Mexico (●, recorded localities); G, overwintering area of the eastern population; H, overwintering area of the western population; K, areas where eastern migrants enter the field of the western population; M, area for which no specimens have been seen or collected; N, possible overwintering site from southern migrants of the western population (as yet not thoroughly investigated).

although release–recapture data from experiments carried out in southern California would indicate this possibility (Urquhart *et al*. 1968).

Although the monarch butterfly occurs in most parts of North America south of 50°N. lat., there is considerable variation in population density. In some areas in Canada, such as British Columbia and Alberta and in the U.S.A. in Arizona and New Mexico, few adult monarch butterflies have ever been collected. In other areas in Canada such as southern Ontario and southern Quebec and in the U.S.A. in the vicinity of the Great Lakes, dense populations occur (Fig. 2). This marked variation in population density is correlated, in part, with the distribution of the various species of milkweed (*Asclepias*) upon which the larvae feed and, in part, to a virus epizootic (Urquhart 1976). Although the North American species of *Asclepias* are found in a wide range of ecological conditions, including desert areas and tropical forests, they are essentially subtropical plants and hence their altitudinal and latitudinal preferences are restricted (Woodson 1954). Only a few hardy species extend to elevations above 2000 m and only six species occur in southern Canada, south of 51°N. lat. Species exhibiting a wide ecological distribution, such as *A. syriaca*, *A. currasavica*, and *A. fascicularis* occur in profusion whereas other species are generally confined to restricted ecological environments where they occur as widely spaced plants. Hence the presence of large populations in the eastern part of North America is due in part to the abundant supply of *A. syriaca* and in the case of the western population to the abundance of *A. currasavica* and *A. fascicularis*.

In addition to the presence or absence of an abundant supply of the larval food plant, the nature of the various species of *Asclepias* also plays an important part. It has been shown that when a larva has been dislodged from its host plant it experiences difficulty in finding another plant and does so by trial and error (Urquhart 1960). If the species of *Syriaca* are widely spaced so that the larva has to wander over a considerable

FIG. 3. Overwintering cluster of the western population in California on the eucalyptus trees and Monterey pines; clusters located at a number of separate sites in California; relatively few in number compared with the mass assemblage in Mexico.

FIG. 4. Overwintering cluster of the eastern population in Mexico on the branches of the Oyamel trees (popularly known as Oyamel mexicana, but taxonomically *Abies religiosa*); two or more clusters occur in separate sites within the same area; owing to the greater breeding area of the eastern population, the number occurring in Mexico is far greater than that in California. (Photograph courtesy National Geographic Society.)

distance to locate another plant, its rate of growth is impeded and it is vulnerable to starvation or predation.

As indicated in Fig. 4 migrant monarch butterflies from the eastern population enter the mountain areas through passes so that there is a gene flow between the two populations and hence there are no morphological variations, as has been suggested by a comparative study of wing lengths (Williams *et al.* 1942). Our studies based on thousands of specimens taken from all parts of the continent indicated no significant difference in wing length (Urquhart 1960).

The release–recapture lines for both the eastern and western populations indicate that a north-east to south-west direction of flight applies to both. It would appear, however, that migrants in the plains regions tend to fly directly south joining the southwesterly route of the migrants from the more eastern areas of the continent towards the overwintering areas in Mexico.

Summary

There are two sympatric populations of monarch butterflies in North America: one occurs east of the Rocky Mountains (eastern population) and the other in the valleys of the Rocky Mountains and west to the Pacific Ocean (western population).

The migrants of the eastern population move southwestward to overwinter in various areas of the Sierra Madre Occidentale mountains of Mexico.

The migrants of the western population move south and southwestward to overwinter in various areas of California.

In areas where the temperature remains high (temperatures below 0°C being rare and of short duration) and where species of *Asclepias* are present, "resident" populations occur which appear to be non-migratory.

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