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WHAT DO MONARCH POPULATION TIME SERIES TELL US ABOUT EASTERN AND WESTERN POPULATION MIXING?

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ABSTRACT. Time series for the annual variation in the size of the central Mexican overwintering population, the California (western) summer breeding population (4th of July Count) and the California coastal wintering population (Thanksgiving Count) are examined. The California summer and following wintering populations are found to correlate with the size of the previous winter's central Mexico population in support of the hypothesis that monarchs migrating north in the spring from Mexico contribute to the western population

Additional key words: *Danaus plexippus*, Annual census, Time series, Climate dependence, Mexico, California

The monarch (*Danaus plexippus*) butterfly has long been of interest because of its remarkable migratory pattern. There are two North American populations of monarchs; one that summers east of the Rocky Mountains and migrates to and overwinters in the mountain forests in central Mexico, and another population west of the Rocky Mountains that winters along the central and southern California coast and disperses east and north in the summer (Urquhart 1987, Brower 1995a).

The recognition of this pattern has arisen and been supported by extensive mark/recapture results, particularly for the eastern population (Monarch Watch). Unlike birds, but similar to the migratory Painted Lady (*Vanessa cardui*) butterfly, any particular individual of the eastern population does not make the complete trip from the wintering grounds to the northernmost summer grounds. Instead the returning overwintered individuals breed along the Gulf Coast and their offspring continue the migration northward (Malcolm *et al.*1993, Knight *et al.*1999). Additional breeding generations complete the northeastern recolonization (Brower 1996). The temporal variation in the recolonization rate has been shown to be remarkably stable from year to year (Davis and Howard, 2005). The return migration to the overwintering areas is made by the final fall generation that enters reproductive diapause (Urquhart 1960) and flies to Mexico (Urquhart and Urquhart, 1978).

The extent to which the two populations may mix is largely unknown. Some mark-release-recapture results (Monarch Watch) have trajectories that hint at mixing. Directions of movement of individuals in the west have also been interpreted as indicating migration paths that might lead to population mixing (Pyle 1999). However mitochondrial DNA sequencing indicates very little heterogeneity between the eastern and western North American populations, and even between the North and South American populations (A. Brower *et al.* 2004). L. Brower and Pyle (2004) have summarized the evidence for some interchange between the eastern and western populations.

The purpose of this study is to examine correlations in year-to-year Monarch fluctuations at the eastern and western population overwintering sites and at western population breeding sites for clues as to whether the western population is supplemented by Monarchs from the eastern population overwintering area in Mexico.

METHODS AND DATA SOURCES

This study makes use of three annual census counts. The first is the 4th of July Butterfly Count, the longest running monarch butterfly monitoring program. It was initiated by the Xerces Society in 1975 and is presently under the auspices of the North American Butterfly Association (NABA). Butterflies within a 15-mile diameter circle are counted. There are five count circles west of the Rocky Mountains for which counts have been performed every year during the last decade, and at which Monarchs are seen on a regular basis. These are Cosumnes River (38 21 N, 121 27 W), Mt. Diablo (37 57 N, 121 52 W), Willow Slough (38 34 N, 121 44 W), Dardanelles (38 22 N, 119 45 W) and San Joaquin Co. (38 9 N, 121 18 W). The number of butterflies observed has been divided by the number of party-hours reported in an attempt to correct for differences in observer effort and coverage from year to year. Issues related to these counts have been discussed by Swengel (1990). Many counts have observers that have participated in a particular count circle for a number of years, helping to make observed changes in butterfly numbers from year to year more accurate. One count circle, Willow Slough, CA, has been counted by the same observer, Art Shapiro, for all but one of the last 27 years (NABA 1999)! The count results are presently published yearly by NABA (4 Delaware Rd., Morristown, NJ 07960).

The second census, the Monarch Program

Thanksgiving Count of the overwintering population in California, is patterned after the 4th of July Butterfly Count, takes place during a 2-week period around Thanksgiving. Approximately 100 overwintering sites in 15 California counties are surveyed. The largest numbers of Monarchs are between San Francisco and Los Angeles. The first count was in 1997. The results for the seven years 1997–2003 have been compiled by Dennis Frey and Shana Stevens and are posted on the Monarch Program website (www.monarchprogram.org/tagging.htm). The results from the first four years have been discussed by Frey and Schaffner (2004). The 1997–2003 data, as well as 4th of July Butterfly Count data for the period 1977–1999 has been examined by Koenig (2006). He looked for spatial synchrony, the extent to which the populations vary in size from year to year in unison over considerable geographical distances. A modest (correlation coefficient about 0.3) but statistically significant correlation was found for the Thanksgiving counts over distances as large as 1000 km. With only three years overlap with his 4th of July data set he did not compare trends between the two data sets.

The third count, the Monarch Butterfly Biosphere Reserve census, estimates the size of the overwintering population in Mexico. The eastern breeding population

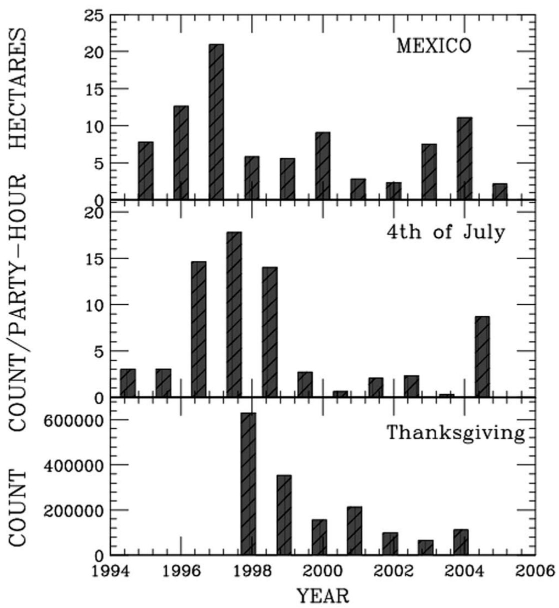

FIG. 1. Comparison of wintering (eastern) population in Mexico (top), California (western) summer population (middle) and California Thanksgiving Count (bottom). The Mexican population size is expressed as hectares occupied. The placement of the bars reflects the time of year at which the census is performed, eg. the bar for the 1996–1997 Mexican wintering population is plotted at 1996.9. The 4th of July data is the sum of the counts/party hour for 5 California sites.

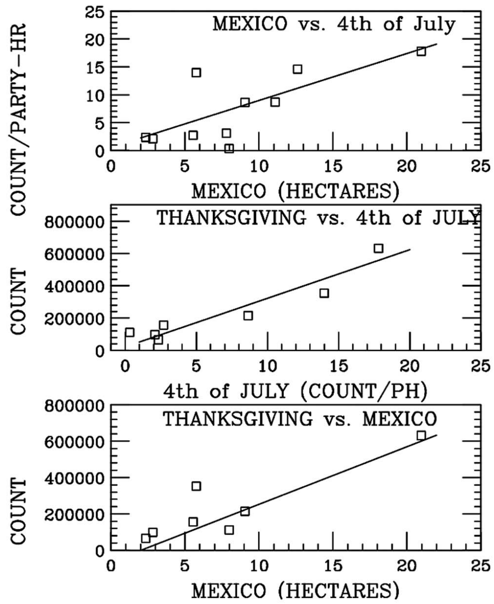

Fig. 2. Regression plots for the three pairs of variables.

of monarchs winter in high-altitude oyamel forests in central Mexico. Garcia-Serrano *et al.* (2004) have described a monitoring program initiated in 1993 under the auspices of the Monarch Butterfly Biosphere Reserve. All known colonies within and outside the reserve are monitored. Rather than attempting to count individual butterflies, the surface area occupied by colonies was measured. The data collection takes place during the last two weeks in December at a time when the colonies have consolidated and are least active. In January an estimate of the mortality at each site was assessed. (This mortality estimate reflects bird and mouse predation as well as mortality due to unknown causes. It does not capture the mortality associated with winter storms that occur later in the winter).

Estimates of the areas occupied by overwintering monarchs are from updates appearing on the Monarch Larvae Monitoring Program (www.mlmp.org) and Journey North (www.learner.org/jnorth/tm/monarch/PopulationMexico.html) websites. Since I am interested in estimating the influence of the size of the wintering population on the following summer and fall monarch numbers, I have reduced by 75% the December count for the 2001–2002 winter due to the severe winter storm in January of 2002 (Brower, Kust *et al*, 2004). There was also a significant winter storm effect on the 2003–2004 winter population but as estimates for the mortality differ greatly (Monarchwatch: www.monarchwatch.org/update/2004/0216.html) I have not attempted a correction for this season.

The largest area occupied by monarchs since the initiation of this project was about 20 hectares (ha) in Dec. 1996. Using previous estimates of butterfly densities of approximately 10 million butterflies/ha (Calvert & Brower 1986, Brower 1995b) would suggest a population of 200 million. More recent density estimates (Brower *et al.* 2004; Calvert 2004) would lead to a much larger population total. During some years however the area occupied by monarchs was only about 1/10th of this.

COMPARISON OF MEXICAN WINTERING POPULATION, CALIFORNIA SUMMER POPULATION, AND CALIFORNIA WINTERING POPULATION TIME SERIES

Population estimates for the Mexican wintering population are available for about a decade and for the California wintering population ("Thanksgiving" count) for seven years going back to 1997. There are five count circles in California where monarchs were regularly observed during the 4th of July Count and for which data are available over the last decade. The count per party hour values for these sites have been added and compared with the Mexican wintering population and the California wintering population estimates in Fig. 1. The most striking observation from this figure is that the California summer population and the California wintering population exhibit a maximum in the summer and fall following the winter with the largest population in Mexico, in spite of the general tenet that the Mexican wintering population remigrates to eastern and central North America via the gulf coast rather than to the west coast.

Multiple regression has been used to explore the correlation between the Mexican wintering population, the 4th of July summer counts, and the California wintering population (Thanksgiving counts). The data used for this analysis are given in Table 1, along with the regression equations obtained. The results of the regression analysis are displayed in Fig. 2. The sum of the count/party-hour for the five California 4th of July counts is found to be strongly correlated with the previous winter's Mexican population, R^2=0.57, p=0.019. The Thanksgiving count is also strongly correlated with the previous winter's Mexican population, R^2=0.78, and p=0.008. As expected from the two previous correlations, the Thanksgiving count correlates well with the 4th of July count/party-hour sum, R^2=0.89, p=0.001. Thus well over half of the fluctuation from year-to-year in the western 4th of July count and the western Thanksgiving count can be explained in terms of the size of the Mexican wintering population.

TABLE 1. Monarch counts from three kinds of censuses. The wintering census in Mexico are characterized by the number of hectares occupied, and are listed for the year in which Jan. of the particular winter occurs. The 4th of July results are the sum of the monarch's per party hour for 5 California sites. The Thanksgiving counts are the number of monarchs observed summed over all sites surveyed.

Year	Mexico	4th of July	Thanksgiving
1994		3.03	
1995	7.8	3.08	
1996	12.6	14.61	
1997	20.97	17.81	631140
1998	5.77	13.99	353272
1999	5.56	2.71	156659
2000	9.05	8.64	214198
2001	2.83	2.08	98418
2002	2.35	2.33	65375
2003	8.0	0.31	111909
2004	11.12	8.69	

Linear regression performed on these data give the following relations:
4th July=0.84 * Mexico + 0.60
Thanksgiving=3,120 * 4th July + 1960
Thanksgiving= 2810 * Mexico + 1410
These relations are illustrated by the straight lines in Fig. 2

Two possible explanations for these strong correlations are: firstly, there is some climate variation effect common to both populations, and, secondly, that the western population is supplemented by monarchs from the Mexican overwintering population. The first possibility does not seem likely as it would seem to require the spring and summer climate in the east to be favorable the year before a favorable spring and summer climate in the west. This requirement arises because the peaks in the summer 4th of July count and the California Thanksgiving count lag the peak in the Mexican count by one half and one year, respectively. A second explanation is that some fraction of the eastern Mexican wintering population may migrate to the west in the spring and contribute to the western population in the following summer and fall. Such a hypothesis was put forward independently by L. Brower and S. Gauthreaux in 1996 (see Brower and Pyle, 2004). Since the eastern wintering population is about two orders of magnitude larger than the western wintering population, it would require only a very small fraction of the Mexican overwintering population to noticeably influence the western breeding and subsequent fall wintering population. Brower and Pyle make the further suggestion that the long-term survival of the western population of monarchs may depend on occasional replenishment from the Mexican winter population. This mechanism may also have enabled an expansion of the western population to exploit changes in coastal tree species distributions in historical times. The western population's wintering grounds are presently primarily in Eucalyptus trees, which are not native to the U.S. and were introduced by settlers in the 1850's (Lane 1993). Lane has reviewed the historical evidence for the use of other tree species by overwintering Monarchs.

SUMMARY

The time correlation of the year-to-year fluctuations in monarch numbers have been examined at several different locations and seasons from which it has been inferred that the western population is supplemented by contributions from the eastern population. This inference, based only on time series correlations, was possible independent of the mechanism responsible for the fluctuations.

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This work complies with the current laws of the United States.

LITERATURE CITED

BROWER, A. V., and M. M. JEANSONN, 2004. Geographical populations and 'subspecies' of new world monarch butterflies (Nymphalidae) share a recent origin and are not phylogenetically distinct. Ann. Entomol. Soc. Am. 97: 519–523.

BROWER, L. P. 1995a. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America, J. Lepid. Society 49:304–385.

BROWER, L. P. 1995b. Revision a los mitos de Jurgen Hoth. Ciencias. 39: 50–51.

BROWER, L. P., 1996. Monarch butterfly orientation: missing pieces of a magnificent puzzle. J. of Experimental Biology 199: 93–103.

BROWER, L. P., E. R. SALINA, E. GARCIA-SERRANO, D. R. KUST, J. MILLER, J. C. FERNANDEZ DEL REY, K. PAPE, 2004. Catastrophic Winter Storm Mortality of Monarch Butterflies in Mexico during January 2002. Pages 151–166 *In* K. S. Oberhauser, M. J. Solensky, editors, The Monarch butterfly: biology and conservation. Cornell University Press, Ithaca, NY.

BROWER, L. P., and R. M. PYLE, 2004. The interchange of migratory monarchs between Mexico and the western United States, and the importance of floral corridors to the fall and spring migrations. Pages 144–166 *In* G. P. Nabhan, editor. Conserving migratory pollinators and nectar corridors in western North America. U. of Arizona Press and the Arizona-Sonora Desert Museum, Tucson, AZ.

CALVERT, W. H., and L. P. BROWER, 1986. The location of monarch butterfly (Danaus plexippus L.) overwintering colonies in Mexico in relation to topography and climate. J. Lepid. Soc. 40:164–187.

CALVERT, W.H. 2004. Two methods estimating overwintering monarch population in Mexico. Pages 121–127 *In* K. S. Oberhauser, M. J. Solensky, editors, The Monarch butterfly: biology and conservation. Cornell University Press, Ithaca, NY.

DAVIS, A. K, and E. HOWARD. 2005. Spring recolonization rate of monarch butterflies in eastern North America: new estimates from citizen-science data. J. Lepid. Soc. 59:1–5.

FREY, D., and A. SCHAFFNER, 2004. Spatial and temporal pattern of monarch overwintering abundance in western North America. Pages 167–176 *In* K. S. Oberhauser, M. J. Solensky, editors, The Monarch butterfly: biology and conservation. Cornell University Press, Ithaca, NY.

GARCIA-SERRANO, E., J. L. REYE, and B. X. M. ALVAREZ, 2004. Locations and area occupied by monarch butterflies overwintering in Mexico from 1993 to 2002. Pages 129–133 *In* K. S. Oberhauser, M. J. Solensky, editors, The Monarch butterfly: biology and conservation. Cornell University Press, Ithaca, NY.

Journey North, http://www.learner.org/jnorth/tm/monarch/PopulationMexico.html

KNIGHT, A., L. P. BROWER, and E. H. WILLIAMS, 1999. Spring remigration of the monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae) in north-central Florida; estimating population parameters using mark-recapture. Biological Journal of the Linnean Society 68:531–556.

KOENIG, W. D., 2006. Spatial synchrony of monarch butterflies. The American Midland Naturalist 155:39–49.

LANE, J., 1993. Overwintering monarch butterflies in California: past and present. Pages 335–344 *In* S. B. Malcolm and M. P. Zalucki, editors. Biology and conservation of the Monarch butterfly. Natural History Museum of Los Angeles County, Los Angeles, CA.

MALCOLM, S. B., B. J. COCKRELL, AND L. P. BROWER, 1993. Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? Pages 253–267 *In* S. B. Malcolm and M. P. Zalucki, editors. Biology and conservation of the Monarch butterfly. Natural History Museum of Los Angeles County, Los Angeles, CA.

MONARCH LARVAE MONITORING PROGRAM, http://www.mlmp.org

MONARCH WATCH, http://www.MonarchWatch.org/

NABA, 1999. "1999 Report, NABA 4th of July Counts", North American Butterfly Association, 4 Delaware Rd., Morristown, NJ 07960, p. iii.

PYLE, R. M., 1999. Chasing Monarchs. Houghton Mifflin, New York.

SWENGEL, A., 1990. Monitoring butterfly populations using the fourth of July butterfly count. The American Midland Naturalist, 124: 395–406.

SWENGEL, , A., 1995. Population fluctuations of the Monarch (*Danaus plexippus*) in the 4th of July Butterfly Count 1977–1994. The American Midland Naturalist 134: 205–214.

URQUHART, F. A., 1960. The Monarch butterfly. U. of Toronto Press, Toronto, Canada.

URQUHART,, F. A., and N. A. URQUHART,, 1978. Autumnal migration routes of the eastern population of the monarch butterfly (*Danaus p. plexippus* L:Danaidae; Lepidoptra) in North America to the overwintering site in the Neovolcanic Plateau of Mexico. Can. J. Zool. 56: 1759–1764.

URQUHART,, F. A., 1987. The Monarch butterfly: international traveler. Nelson-Hall, Chicago.

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