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Spring remigration of the monarch butterfly, *Danaus plexippus* (Lepidoptera: Nymphalidae) in north-central Florida: estimating population parameters using mark-recapture

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Monarch butterflies (*Danaus plexippus*) of the eastern North American population migrate each fall from the northern U.S.A. and southern Canada to overwintering sites in Mexico and return the following spring to the southeastern U.S.A. where they lay eggs and then die. The spring remigration is the least studied phase in the annual migration cycle. We therefore conducted a mark-recapture study and examined population recolonization dynamics and residence time in a north-central Florida pasture where the monarch's milkweed host plant (*Asclepias humistrata*) was abundant. Beginning in late March 1995 two waves of monarchs arrived, their numbers peaked at 71 individuals by mid-April, and the butterflies disappeared in early May. After arriving, the adults remained for 3–5 days, laid eggs and then continued to migrate. We also compared population sizes and arrival times in 1994 and 1996. We found no evidence of a second spring generation, which was also consistent with the deteriorating quality of the *A. humistrata* plants. Individuals of the new spring generation disappear shortly after eclosion. The arriving population was approximately nine times greater in 1995 than in 1996. Our findings support two recent hypotheses: (1) the bird-like migration of the monarch butterfly in North America evolved with the northward expansion and phenology of milkweeds; and (2) monarchs appear to be migratory throughout their annual cycle of several generations. By lingering for only a short time at each milkweed patch they encounter, the old monarchs returning from Mexico locate the resurgent milkweed flora over an extensive area in the southern states. Then, within less than a month, their fresh offspring continue the migration and exploit the unfolding cornucopia of milkweeds as

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the spring advances northward. The more we discover about the biology of this insect, the more remarkable is its annual migratory, breeding and overwintering cycle.

ADDITIONAL KEY WORDS:—evolution of butterfly migration – residence time – Mexico – Gulf Coast states – Eastern North America – population dynamics.

CONTENTS

INTRODUCTION

The monarch butterfly (*Danaus plexippus* L., Nymphalidae) exhibits enormous intraspecific variation in its population structure and dynamics. These include continuously breeding resident populations in south Florida (Knight, 1998), the Caribbean, and Central and South America (Urquhart, 1960; Urquhart & Urquhart 1976; Janzen, 1983; Ackery & Vane-Wright, 1984; Haber, 1993) and long-lived migratory populations in North America, both east and west of the Rocky Mountains, in which individuals spend up to 6 months in reproductive dormancy (Herman, 1973; Barker & Herman, 1973; Brower, 1985). Within the eastern North American population, three to four spring and summer breeding generations are produced, with some exposed to temperature regimes and host plant species different from those encountered by their progeny (Malcolm *et al.*, 1987; 1993; Brower, 1996).

Few studies have been done on the structure and dynamics of breeding populations of monarchs (Malcolm *et al.*, 1987). Mark-recapture studies have been done in Australia (Zalucki & Kitching, 1984; Zalucki & Suzuki, 1987) where both monarchs and their food plants had become established by 1870 (Vane-Wright, 1993). It may be argued, however, that because the populational origins both of the founding monarchs and their milkweed foodplants in Australia are unknown, interpretations of their population biology may differ from North American monarchs.

The eastern North American monarch population

Each autumn monarch butterflies east of the Rocky Mountains migrate from their breeding range in southern Canada and the northeastern and central U.S.A. to overwintering sites in high elevation conifer forests of central Mexico. Before beginning their southward journey, monarchs emerging in late summer and early autumn enter reproductive diapause (Urquhart, 1960), a period when various reproductive organs exhibit a reduced response to favourable, summer-like breeding conditions (Herman, 1981). Although diapause in monarchs is associated with changes in photoperiod and temperature, the relative roles of these factors and the induction, maintenance, and termination of diapause are not well understood (Barker & Herman, 1976; Herman, 1981). After reaching Mexico in early November, the monarchs spend the winter in a semi-dormant state, clustering by the millions in Oyamel fir trees (*Abies religiosa* H.B.K. Schl. & Cham., Pinaceae) that serve as a thermal blanket and umbrella for protection against freezing and wetting (Anderson & Brower, 1996). The estimated density of monarchs in the Mexican overwintering sites is approximately 10 million butterflies per hectare, with some colonies up to 3.34 ha in extent (Brower & Calvert, 1986).

With the approach of the spring equinox, reproductive diapause ends and the overwintering clusters begin to break apart (Herman, 1981, 1986; Herman *et al.*, 1993; Van Hook, 1996). A mass mating event ensues, although many females begin the spring remigration without having mated (Van Hook, 1996). From mid-March to early April both sexes migrate to the Gulf Coast states, continue to mate and the females oviposit upon the newly emergent spring milkweeds. Malcolm *et al.* (1993) determined through cardenolide fingerprinting of the butterflies that recolonization of the northern breeding range is accomplished primarily by the northward and northeastward migration of the subsequent new generation of monarchs produced in the Gulf Coast states. The extent to which the remigrating monarchs from Mexico continue moving northward after encountering and laying eggs on the southern milkweeds has never been quantitatively studied, although a few remigrants do make it as far north as Maryland and Kansas (Fales, 1984; Brower, 1995).

Spring remigration to north-central Florida

Successful establishment of a new spring generation is inextricably linked to the arrival time of remigrants in the Gulf Coast states. If monarchs arrive too early in March, frost may kill back the milkweeds, leading to starvation of newly hatched larvae (Brower, unpublished data). If they arrive too late, i.e. mid to late April, the milkweeds will have begun to become senescent (this study). Hence, there is only about a 3 week window when monarchs can successfully establish the new spring generation. Malcolm *et al.* (1993) provided evidence that the remigrants from Mexico arrive almost simultaneously in the Gulf Coast states from Texas to Florida, but that the number of remigrants decreases eastward. Consequently, the remigration into Florida is small in comparison to that farther west along the Gulf Coast states of Texas and Louisiana (Cockrell *et al.*, 1993; Lynch & Martin, 1993; Malcolm *et al.*, 1993; Riley 1993). The fact that very few monarchs are found east of the Appalachians in June and July compared to the Midwestern states supports the idea that the first spring generation is produced largely in Texas and Louisiana rather than in the more eastern Gulf Coast states (Brower, 1996).

Although Florida is the easternmost edge of the spring remigration, observations made since 1981 have indicated that monarchs consistently return each March to north-central Florida, where females oviposit on *Asclepias humistrata* L. (Asclepiadaceae), the sandhill milkweed (Cohen & Brower, 1982; Malcolm *et al.*, 1987, 1993; Cockrell *et al.*, 1993; Zalucki & Brower 1992). This milkweed occurs naturally in well drained sandhill areas and in dry oak forests and pine-scrub habitats from North Carolina to central Florida and westward to Louisiana (Woodson, 1954; Clewell, 1985; Wunderlin, 1982; Bell & Taylor, 1982. In north-central Florida it is also found in overgrazed, well-drained sandy pastures (pers. observ.).

Cardenolide fingerprint analyses of 159 adult monarchs (Knight, 1998) captured in north-central Florida in March and April during the 1980s and 90s showed that at least 69% had fed as larvae on *Asclepias syriaca* L., a milkweed that occurs across the monarch's summer breeding range in the northeastern U.S.A. Because *A. syriaca* does not naturally occur south of Virginia (Woodson, 1954), the fingerprint analyses confirmed that the majority of the early spring monarchs in north-central Florida (1) had to have developed in the north during the previous summer and (2) and were spring remigrants that had overwintered rather than a new generation of monarchs produced in southern Florida or elsewhere in the tropics. (If the latter, they would have exhibited the *A. curassavica* cardneolide fingerprint; Knight and Brower, in prep.). These data, together with over a century of natural history observations (Brower, 1995), indicate that most of the north-central Florida monarchs had overwintered in Mexico.

This study

Our study focuses on monarchs that returned from their Mexico overwintering sites in 1994–1996 to a 1 ha pasture with abundant *A. humistrata* milkweeds in north-central Florida. These monarchs represent a sample of the migratory eastern monarch population which may be considered effectively panmictic because the butterflies' migration and aggregation behaviours thoroughly mix the adults prior to their mating at the end of the overwintering period (Van Hook, 1993; Wassenaar & Hobson, 1999). Although we refer to the Cross Creek monarchs as a population, they clearly are not genetically isolated from the rest of the eastern population. We use the term population as loosely defined by Krebs (1994: 151) as "a group of organisms of the same species occupying a particular space at a particular time."

Our purpose was to determine basic population characteristics of spring remigrants flying from their overwintering area in Mexico to a breeding site in north-central Florida. Specifically, we addressed the following questions: (1) How large does the north-central Florida population become during the spring remigration and how does it change as spring progresses? (2) Do monarchs arrive in one or several waves? (3) Is the remigrant population augmented by emergence of the new generation of offspring? (4) Do the remigrants lay all their eggs once they encounter a substantive milkweed patch and die, or do they continue migrating northward? (5) Do the sexes have similar residence times in the milkweed patch? (6) How do the numbers of butterflies and their arrival times vary from year to year?

METHODS

We used mark-recapture population estimates, wing wear data, and egg and larval census data in 1995 to investigate the questions listed above. We also compared relative population sizes for 1995 and 1996 using the number of adult monarchs caught per person hour. Additionally, we conducted comparative egg and larval censuses during 1994–1996.

The study site

Our 'Cross Creek' study site was located in Alachua County in north-central Florida, approximately 20 miles SE of Gainesville (29°32′N; 82°11′W) near the town of Cross Creek and consisted of a cattle pasture (ca. 1 ha) containing several hundred sandhill milkweed plants, *A. humistrata.* Several large longleaf pines, *Pinus palustris* Mill. (Pinaceae) were scattered through the pasture which had not been treated with herbicide, allowing the establishment of *A. humistrata* as well as other herbaceous species undesirable for cattle, including prickly pear cactus, *Opuntia humifusa* Raf. (Cactaceae), tread softly, *Cnidoscolus stimulosus* (Michx.) Engelm. & Gray (Euphorbiaceae), and yellow thistle, *Cirsium horridulum* Michx. (Compositae). The site was bounded on the north, east and west by 'improved' grass pasture that contained virtually no milkweeds or other nectar sources, and to the south by County Road 345 and a commercially planted slash pine, *Pinus elliottii* Engelm. (Pinaceae) forest. A 20 m wide strip of mature live oaks, *Quercus virginiana* Mill. (Fagaceae) separated the site from the neighboring pasture to the east.

Although scattered *A. humistrata* plants occur in the upland habitats of the nearby Lochloosa forest as well as along the well-drained sandy road margins in this area of north Florida, the large, dense milkweed patch at our Cross Creek site is relatively isolated. We surveyed pastures in southern Alachua County and in adjacent portions of Levy, Marion, and Putnam Counties. None had more than a few *A. humistrata.* Other species of milkweed occur in the area, but are scattered, localized and much less abundant (Woodson, 1954; Moranz & Brower, 1998).

Mark-recapture techniques

Our mark-recapture study was conducted from 26 March to 30 April 1995. We captured monarchs daily (except on 3 rainy days) from 26 March to 12 April and then approximately every other day until 30 April (Table 1, but see 'Population estimates' below for why we deleted 1 April). Butterflies were netted for a 1 h period by one person between 10:00 and 13:00 h eastern daylight time. Two exceptions were 27 March when two persons captured for a total of 1.3 h and 2 April when

Table 1. Leslie and Chitty's (1951) 'Method B Table' for mark-recapture data for monarch butterflies captured during the spring of 1995 at Cross Creek, Florida. Rain precluded sampling on March 31, April 5, and April 27. If none of the recaptured butterflies on a particular sampling day had been caught on the previous sampling day, then no estimate could be calculated for that day, and it was deemed an untestable day. The only untestable day for the entire population was April 1 and this table reflects its elimination. (See 'Population estimates' in Methods)

		First Recaptured																							
		Mar 26	Mar 27	Mar 28	Mar 29	Mar 30	Apr 2	Apr 3	Apr 4	Apr 6	Apr 7	Apr 8	Apr 9	Apr 10	Apr 11	Apr 12	Apr 14	Apr 16	Apr 17	Apr 19	Apr 21	Apr 23	Apr 25	Apr 28	Apr 30
Last Recaptured	26-Mar		7	1	1	1	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	27-Mar			2	3	0	0	0	0	1	0	0	0	0	0	1	0	0	0	0	1	0	0	0	0
	28-Mar				3	0	2	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	29-Mar					6	5	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	30-Mar						6	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
	2-Apr							7	5	2	1	1	0	1	0	1	0	0	0	0	0	0	0	0	0
	3-Apr								7	1	1	0	0	2	0	0	0	0	0	0	0	0	0	0	0
	4-Apr									6	1	1	3	1	0	0	0	0	1	0	0	0	0	0	0
	6-Apr										2	3	2	1	0	1	1	1	0	0	0	0	0	0	0
	7-Apr											1	3	1	0	0	0	0	0	0	0	0	0	0	0
	8-Apr												6	2	0	0	0	1	0	0	0	0	0	0	0
	9-Apr													8	1	1	0	0	1	1	0	0	0	0	0
	10-Apr														4	0	2	1	1	0	0	0	0	0	0
	11-Apr															1	0	1	1	0	0	0	0	0	0
	12-Apr																1	1	1	0	0	0	1	0	0
	14-Apr																	2	1	1	0	0	0	0	0
	16-Apr																		1	0	0	1	0	0	0
	17-Apr																			1	1	0	0	0	0
	19-Apr																				1	0	1	0	0
	21-Apr																					2	1	0	0
	23-Apr																						1	0	0
	25-Apr																							1	0
	28-Apr																								1
	30-Apr																								
Tot Marked		0	7	3	7	7	14	8	12	10	5	6	14	16	5	5	4	7	7	3	3	3	4	1	1
Tot Unmarked		16	9	5	14	9	24	7	9	8	3	4	5	1	4	3	4	2	1	1	3	3	1	1	1
Tot Caught		16	16	8	21	16	38	15	21	18	8	10	19	17	9	8	8	9	8	4	6	6	5	2	2
Tot Released		16	16	8	21	16	38	15	21	18	8	10	19	17	9	8	8	9	8	4	6	6	5	2	2

two persons captured for a total of 2 h. No adult monarchs were seen in the pasture at the end of the sampling periods. Upon capture, each butterfly was placed in a glassine envelope and held in a cooler containing artificial ice packets. At the end of the collection period, each unmarked monarch was sexed, tagged with a numbered, gummed label that was press-applied to the right forewing, and its wing condition was recorded in increments of 0.5, from 1 (very fresh, virtually no scales missing) to 5 (very worn, many scales missing). Individual numbers, sex and condition of recaptures were also recorded. We then rechilled all the butterflies in the cooler for about 10 minutes and individually placed them on Live Oak trunks in the shade to minimize escape responses that might cause them to leave the study site. Within about 5 minutes, the butterflies warmed to flight threshold and resumed normal activity.

In 1996 the method was modified as follows: the capture effort was less intense (monarchs were captured every 3 to 4 days from 3 April through 12 May), and instead of tagging, the monarchs were given identification numbers with a permanent ink (Sharpie™) marker on the lower right hindwing.

Egg and larval censuses

Milkweeds were censused for eggs and larvae in the springs of 1994–1996. In 1994 and 1996 we censused plants along 2 m wide transects until we had censused at least 50 but not more than 100 plants. The starting points and directions of these transects were selected haphazardly. In 1995 we assigned N–S and E–W coordinates 10 m apart on a 325 m × 142 m grid. A set of coordinates and a compass direction (N, S, E or W) was chosen randomly, and a minimum of 50 and a maximum of 100 plants was surveyed per census. If sampling along a transect reached the edge of the grid before 50 plants were counted, additional transects were randomly selected and censused until this minimum was attained. All leaves, flowers, and buds on all stems of each plant were examined for eggs or larvae two to three times each week. The phenological stage of the plant, the number of stems and the instar and number of larvae and eggs were recorded for each plant.

Adult data analyses

Because our analysis indicated that the Cross Creek monarch population is open with both immigration and emigration occurring, we used the standard mark-recapture method for open populations, i.e. the Jolly–Seber model (Jolly, 1965; Seber, 1973). This model provides estimates of daily population size and daily residence rate, which is the probability that an individual neither dies nor emigrates but stays alive in the study site. Because death and emigration cannot be separated in open populations, we use the term 'residence' rather than 'survival' throughout this paper, following Watt *et al.* (1977) and Tabashnik (1980).

We tested the model assumptions that all individuals must be equally catchable and that the probability of survival (residence, see above) must be independent of age, but can vary from day-to-day (Krebs, 1989). All statistical tests, except for the population models discussed below, were performed using Statview 4.01 (Abacus Concepts, Inc., 1992–93) on a Macintosh computer. Detailed descriptions of these methods are in Knight (1998).

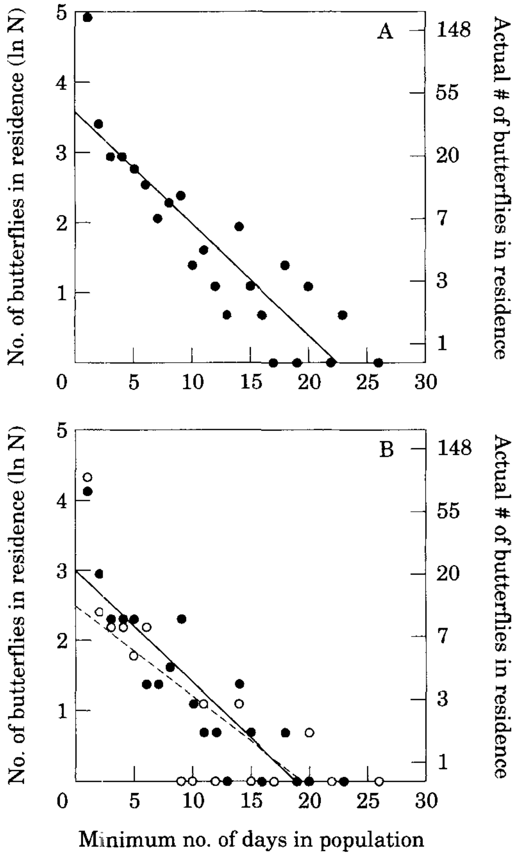

Figure 1. Recapture decay plots for monarch butterflies at the Cross Creek milkweed site in March-April 1995 for (A) the entire population and for (B) males (●) and females (○) separately. N= number of butterflies alive in the study site. All captured individuals spent a minimum of "0" days in the population, i.e. equivalent to ≤ 1 day. The slope of the regression line is the natural logarithm of the daily residence rate. The significant negative slopes indicate a constant rate of loss from the population (Watt *et al.*, 1977). The maximum residence time for males and females was, respectively, 23 and 26 days. The mean residence time for males and females was, respectively, 6.4 and 8.0 days, and the overall average residence time was 4.3 days.

Tests of model assumptions

Begon's method (1979) for marking mortality revealed that the initial tagging did not significantly affect the probability of recapture ($\chi^2 = 0.43$, df= 1, P=0.51). We also used the Leslie, Chitty and Chitty method (Leslie *et al.*, 1953; Krebs, 1995) to estimate the number of new individuals added to the marked population each day and compared this sum with the observed sum of newly marked butterflies to test the validity of the equal catchability assumption. With the exclusion of one anomalous day (April 2, see Knight, 1998), the difference between the observed and estimated number of newly marked individuals was only 6%, a reasonable approximation of equal catchability.

We also tested whether marked individuals were more or less likely to be recaptured than unmarked individuals using a contingency table (Begon, 1979). The results indicated that marking had no effect on catchability ($\chi^2 = 7.24$, df= 5, $0.10 < P < 0.50$).

Equal catchability of males and females was tested by the two methods of Tabashnik (1980): (1) a test of the capture sex ratio *vs.* estimated sex ratio and (2) the joint residence-catchability test. On 7 of the 9 testable days, catchability appeared to be higher for males than for females, but the difference was not statistically significant (Test 2: y intercept $=0.095$, $t=0.43$, $P=0.67$).

The assumption that residence rate (survivorship) is independent of age was tested with recapture decay plots: a regression of the natural logarithm of the number of individuals in the population on the minimum number of days individuals remained in the population (Watt *et al.*, 1977). The regressions (Fig. 1) for the total population, as well as for males and females separately, are highly significant: for the total, slope $= -\ 0.16$, $F_{1,21}=79.95$, $P < 0.0001$; for males only: slope $= -0.16$, $F_{1,18}=59.12$, $P < 0.0001$; and for females only: slope $= -0.13$, $F_{1,20}=29.21$, $P < 0.0001$). These data indicate a constant loss rate that is independent of age (Deevey, 1947).

Residence time

Daily residence rates for the 1995 population, as well as for males and females separately, were calculated by three methods: (1) the weighted average of residence estimate (Jolly, 1965), (2) the recapture decay plot (Watt *et al.*, 1977) and (3) the mean minimum lifespan (Zalucki & Kitching, 1984; Ehrlich & Gilbert, 1973). The joint-residence catchability test (Tabashnik, 1980) was used to test the residence rate of males relative to females.

(1) The weighted average of residence estimate $\emptyset_J$) takes into account all individuals captured at least once and uses the Jolly–Seber daily residence estimate Øi, which we used to represent residence rate. The daily estimates of Øi were multiplied by the inverse of their standard errors (Cook *et al.*, 1967). To normalize these weighting factors, each was divided by the average of all standard-error inverses. This method emphasizes those daily estimates of Øi that have smaller standard errors and thus are derived from the more robust data. We also applied Scott's method II (Scott, 1973) which corrects for gaps in the sampling period. Mean days residence per week and for the entire study period was calculated as $-(\ln\emptyset)^{-1}$ (Cook *et al.*, 1967).

(2) The recapture decay plot method is a regression of the natural logarithm of the number of individuals in the population on the minimum number of days individuals remained in the population. The natural logarithm of the daily residence rate, $\emptyset_D$, is equal to the slope of the regression line. Mean days residence for $\emptyset_D$ was calculated as $-(\ln\ \emptyset)^{-1}$ (Cook *et al.*, 1967).

(3) The mean minimum lifespan method, $\emptyset_L$ eliminates individuals that were not recaptured. Because the Cross Creek monarch butterfly population is migratory, we expect that some individuals moving through will not be recaptured; thus, this method will reflect residence time for individuals whose migratory behaviour has been interrupted for at least 2 days.

Population estimates

Population size in 1995 was estimated with the computer program JOLLY (Krebs, 1995). As a required preliminary to this method, we cast the data (Table 1) in a so-called Method B table (Leslie & Chitty, 1951). Males and females were also analysed

TABLE 2. Mark-recapture data for adult monarch butterflies collected at Cross Creek, Florida from 26 March through 30 April 1995

	Total number marked	Total number of capture events	% recaptured	Mean captures Per individual
Male	61	145	65.6	2.4
Female	76	157	47.4	2.1
Total	137	302	55.5	2.2

separately. These estimates were summed and compared to the Jolly–Seber estimates for the total population using a Wilcoxon signed rank test in order to test the reliability of the independent estimates for each sex.

Population estimates could not be calculated for all sampling dates. If none of the recaptured butterflies on a particular sampling day had been caught on the previous day, then no estimate could be calculated for that day, and it was deemed an untestable day. In such cases, the untestable day was eliminated from the analysis and all butterflies captured on that day were reclassified (see Knight, 1998). The only untestable sampling date for analysis of the entire population was 1 April which coincided with a weather front. The butterflies captured on this day most likely moved through with frontal winds and, thus, were not recaptured. The elimination of this day is reflected in the Method B (Table 1), but it is not reflected in statistical tests that did not directly use this table. There were more untestable dates when the data were broken down to test males and females separately. We could not calculate population estimates for males after 11 April. Thus, male and female population sizes were compared only on matching sample dates from 27 March to 11 April.

In order to detect incoming waves of monarchs, we plotted the Jolly–Seber estimate of number joining over time. Also, the average wing condition at first capture was calculated for combined 3-day intervals and plotted against time (Fig 4).

Insufficient data in 1996 prevented use of the Jolly–Seber model. Therefore, for both 1995 and 1996, a relative population estimate for between year comparisons was calculated as the number of monarch adults caught per person hour. Egg and larval densities were compared for 1994, 1995, and 1996 by plotting the mean number of immatures per milkweed stem over time for all three years.

RESULTS

Numbers marked and recaptured

The basic data for 1995 are summarized in Table 2. From 26 March to 30 April 137 monarchs were netted and marked. Of these there was an insignificant excess of females (76 of 137, 55.5%), but a higher percentage (65.6%) of males was recaptured. Overall 55.5% of all monarchs were recaptured. The mean number of captures per butterfly was 2.4 for males and 2.1 for females. The percentage of monarchs captured each day that were recaptures fluctuated between 33% and 47% from 27 March to 2 April, with the exception of 1 April when it dipped to

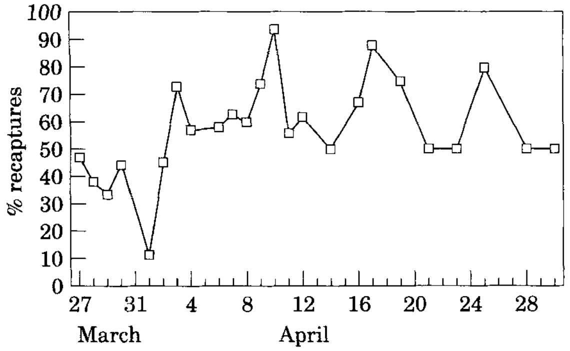

Figure 2. Daily percentage of adults captured that were recaptures.

TABLE 3. Mean residence rate[a] and mean residence time (days) as estimated by three separate methods, b, c, and d (Cross Creek, March–April 1995)

	Estimated Mean Residence					
	$\emptyset_J$[b]		$\emptyset_D$[c]		$\emptyset_L$[d]	
	rate[a]	days	rate[a]	days	rate[a]	days
Males[e]	0.736	3.26	0.856	6.41	0.843	5.84
Females[e]	0.804	4.57	0.882	8.00	0.858	6.55
Females[f]	0.769	3.81				
Total	0.795	4.31	0.856	6.37	0.850	6.15

[a] Residence rate is the probability that an individual in the population on a given sample day will be in the population on the following sample day.

[b] Weighted average of residence estimate (Cook *et al.*, 1967).

[c] Recapture decay plot (Watt *et al.*, 1977).

[d] Mean minimum lifespan (Ehrlich & Gilbert, 1973).

[e] Residence averaged over all testable sampling dates, 26 March–11 April.

[f] Residence averaged over all testable sampling dates for females, 26 March–25 April.

11% (Fig. 2). The percentage of recaptures then fluctuated between 50% and 94% through 17 April, after which samples sizes were too small (<7/day) for meaningful values.

Residence time in the Cross Creek population

The maximum residence time was 26 days for one female and 23 days for a male (Fig. 1). Mean residence for the total population was 4.31 days, as estimated by the weighted average of residence method, $\emptyset_J$ (Table 3). This seems a reliable measure because our data well fit the Jolly–Seber method. Residence estimates by the recapture decay plot, $\emptyset_D$, and the mean minimum lifespan, $\emptyset_L$, were higher, at 6.37 and 6.15 days, respectively. The higher residence time estimated by $\emptyset_L$ was expected because this method excludes butterflies that were captured only once (Ehrlich & Gilbert, 1973). The estimates by $\emptyset_L$ and $\emptyset_D$ are similar, which suggests that mean residence overall is overestimated by $\emptyset_D$. All three methods agree, however, that mean residence time was low (conservatively 4–6 days) for the

TABLE 4. Numbers of monarchs captured per person hour and the Jolly–Seber estimate of the daily adult population size in March and April, 1995 for males and females separately and for the total population. Dashes represent untestable sampling dates on which none of the recaptured butterflies had been caught on the previous sampling day. No estimate could be calculated for that day. See Methods for details. Standard errors are in parentheses

	Number captured per person hr.			Number estimated		
Date	Males	Females	Total pop.	Males	Females	Total pop.
26 Mar	10.0	6.0	16.0	–	–	–
27 Mar	6.2	5.3	11.5	15 (5)	14 (7)	31 (9)
28 Mar	5.0	3.0	8.0	10 (4)	–	37 (18)
29 Mar	10.0	11.0	21.0	17 (5)	56 (44)	55 (18)
30 Mar	11.0	5.0	16.0	23 (7)	–	65 (24)
1 Apr	5.0	4.0	9.0	–	–	–
2 Apr	9.0	10.0	19.0	20 (4)	50 (25)	58 (12)
3 Apr	11.0	4.0	15.0	18 (4)	–	47 (12)
4 Apr	11.0	10.0	21.0	18 (4)	51 (30)	55 (12)
6 Apr	8.0	11.0	19.0	32 (16)	23 (7)	61 (16)
7 Apr	2.0	6.0	8.0	–	21 (8)	57 (21)
8 Apr	5.0	5.0	10.0	19 (7)	21 (8)	46 (12)
9 Apr	7.0	12.0	19.0	31 (18)	21 (6)	52 (11)
10 Apr	8.0	9.0	17.0	11 (5)	24 (11)	42 (10)
11 Apr	3.0	6.0	9.0	5	26 (17)	71 (38)
12 Apr	3.0	5.0	8.0	–	–	43 (18)
14 Apr	4.0	4.0	8.0	–	16 (13)	49 (23)
16 Apr	4.0	5.0	9.0	–	9 (7)	50 (31)
17 Apr	3.0	5.0	8.0	–	2 (1)	25 (14)
19 Apr	3.0	1.0	4.0	–	3 (1)	12 (7)
21 Apr	3.0	3.0	6.0	–	2 (1)	14 (7)
23 Apr	4.0	2.0	6.0	–	2 (1)	24 (22)
25 Apr	3.0	2.0	5.0	–	1 (1)	5 (2)
28 Apr	1.0	1.0	2.0	–	–	2 (1)

remigrants at Cross Creek, and that females, on average, were in residence about 1 day longer than males. The joint residence-catchability test indicated that the residence difference between the sexes was not significant (slope $= -0.016$, $F_{1,11} = 0.14$, $P = 0.71$; Fig. 1).

The weekly $\emptyset_{\mathrm{J}}$ estimates indicated that mean residence time varied throughout the study period. During the first week (March 26–April 1) it was 3.92 days; during the second (April 2–8) it was 6.82 days; during the third (April 9–15) it decreased to 1.89 days; and during the fourth (April 16–22) it was 2.91 days.

The overall $\emptyset_{\mathrm{J}}$ estimate of 4.31 days is higher than the mean residence estimates for either males (3.26 days) or females (3.81 days). Note that the testable sampling dates differ for the males and females: 26 March–11 April and 26 March–25 April, respectively. The data thus suggest that smaller samples underestimate residence time.

Population estimates and waves of new arrivals

The accuracy of the Jolly–Seber population estimate depends on how well the Cross Creek population approximates the assumptions of the model. All assumptions for the most part were upheld which suggests that the daily population size estimates are reliable (Table 4; Fig. 3). The reliability of the Jolly–Seber estimates is further

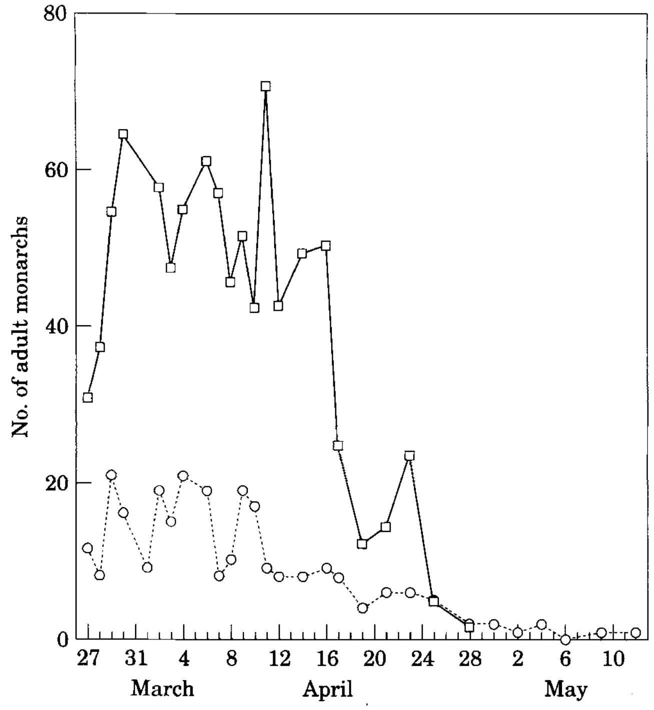

Figure 3. Comparison of two estimates of the daily adult monarch butterfly population size at the Cross Creek milkweed site during March and April 1995: (1) the Jolly–Seber estimate, based on mark-recapture; and (2) monarchs caught per person hour. (□) Jolly–Seber estimate; (○) No. per person hour.

strengthened by the high percentage of captures that were previously marked (Fig. 2). In 1995 the Cross Creek monarch population increased from about 30 individuals on 27 March to 65 individuals on 30 March (Fig. 3, Jolly–Seber line). Thereafter the numbers fluctuated around 55 individuals through 16 April, reaching a peak of 71 on 11 April. The population declined rapidly through the rest of April. The number of butterflies caught per person hour was significantly correlated with the number estimated by the Jolly–Seber method ($r^2 = 0.47$, $F_{1,20} = 17.64$, $P < 0.001$).

There was no difference between the total population estimate and the summed estimates of males and females (Wilcoxon signed rank test, $z = -0.06$, $P = 0.95$), which suggests that the Jolly–Seber population estimates for males and females *per se* are reliable. Accordingly, females were more than twice as abundant as males for most of the matching sampling dates (27 March–11 April; Table 4; Fig. 5A). This differs from more permanent breeding populations in Australia (Zalucki, pers. comm.). The actual numbers of males and females captured per person hour at Cross Creek (Fig. 5B) do not reflect the higher recapture rate for males through most of the sampling period. This accounts for the discrepancy in sex ratio between the number captured (Fig. 5B) and the number estimated in the population (Fig. 5A).

Another objective was to identify waves of incoming monarchs. From the Jolly–Seber estimate of number joining, it appears that a first wave formed the Cross Creek population during the last week of March, with a peak during 27–30 March

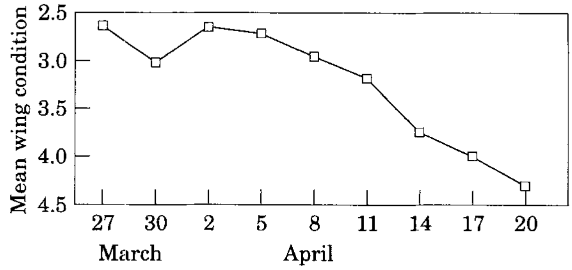

Figure 4. Wing condition of newly captured monarchs averaged over three-day intervals. Wing condition was rated from 1 (freshly eclosed with virtually no scales missing) to 5 (very worn with many scales missing). Each average was calculated with a minimum of three individuals.

(Fig. 6). This is supported by a dip in percentage captures that were recaptures during this period (Fig. 2). These findings are consistent with previous observations that the spring remigrants begin arriving at Cross Creek in mid to late March. A second wave of incoming monarchs occurred from 10 to 12 April (Fig. 6). This is supported by a drop in recaptures from 94% to 56% (Fig. 2). The Jolly–Seber estimate indicates very few individuals joining after 12 April, and the small sample sizes after 16 April preclude accurate treatment of these data.

Another way to detect waves of new monarchs is to look at wing condition changes over time (Fig. 4). Assuming that wing condition is fairly good for individuals upon arrival from Mexico, we predicted that successive waves of new arrivals would result in periodic increases (lower score) in mean wing condition. Mean wing condition of new captures was best for the periods 26–28 March and 1–3 April (Fig. 4), the first of which corresponds to the early peak of the Jolly–Seber estimate of the number joining (Fig. 6). Mean wing condition then deteriorated slowly until 10–12 April, after which it dropped off more sharply. This drop corresponds to the Jolly–Seber estimate of 12 April (Fig. 6), after which few butterflies joined the population. The new wave on 10 April indicated in Figure 6, was not reflected by a fresher mean wing condition (Fig. 4). The population size, however, reached its maximum of 71 individuals (according to the Jolly–Seber population estimate) on 11 April (Fig. 3). Because the population at this time was comprised of many butterflies with varied wing conditions, an increase in mean wing condition due to the arrival of newer butterflies may have been dampened, and the butterflies that joined may have 'aged' while spending more time before getting to Cross Creek.

Monarch population size compared among three years

The mean daily monarch population size at Cross Creek, as estimated by number of butterflies caught per person h, was 9.4 times greater in 1995 than in 1996 (means = 16.9 and 1.8, respectively; Fig. 7A). The number of eggs and larvae per stem was also lower in 1996 than in 1994 and 1995 (Fig. 7B). Numbers of immatures, primarily eggs, also peaked at different times for the different years. The maximum number of eggs was found on 29 March in 1995 (1.55 immatures/stem), on 6 April in 1996, (0.27 immatures/stem), and on 10 April in 1994 (1.23 immatures/stem). These data imply that the arrival of spring migrants was at least a week earlier in 1995 than in 1994 or 1996.

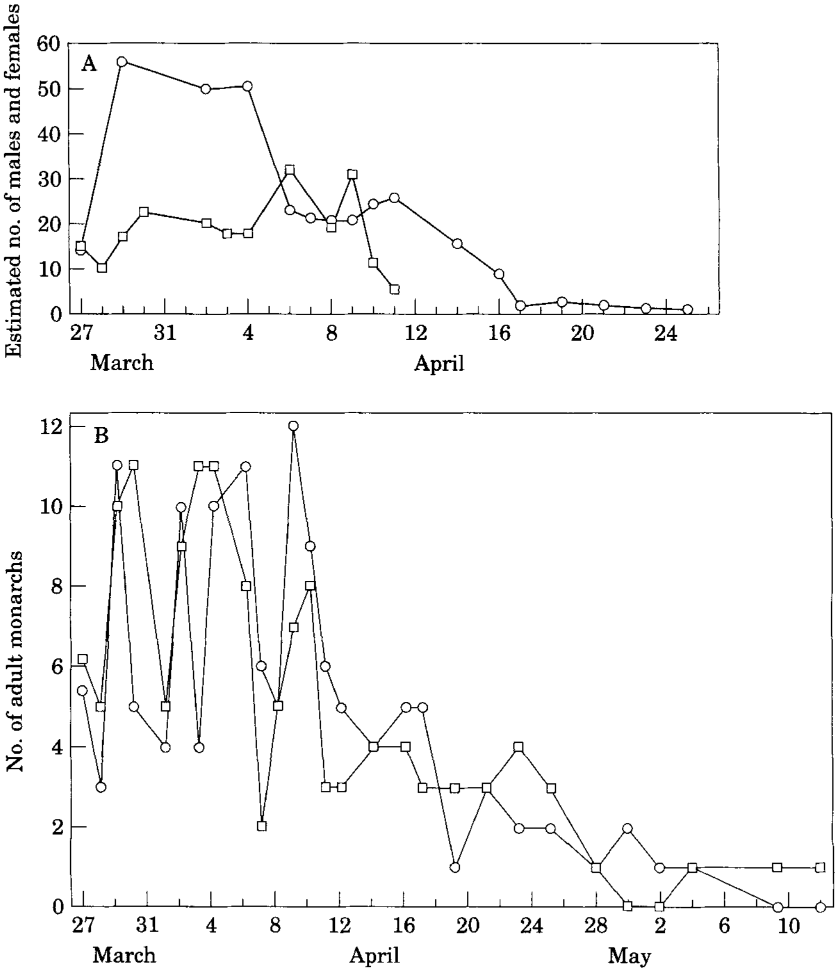

Figure 5. Comparison of male and female daily numbers at Cross Creek in 1995 by two estimates: A, Jolly–Seber estimates; the testable sampling dates (dates with sufficient data) were 27 March–11 April for males and 27 March–25 April for females. B, number caught per person hour. No adults were seen after 12 May. (□) males; (○) females.

The first new spring generation

If a monarch of the new spring generation were captured several days after eclosion, its wings would show some wear, and it might not be distinguishable from a remigrant. Very fresh butterflies (wing condition 1.0 or 1.5), however, would presumably be recently eclosed members of the first new spring generation. We captured only four such individuals in 1995. Two of these were caught on 23 and 30 April, which is consistent with peak egg-laying by remigrants in our area during the last week of March. This would result in eclosion of a first new spring generation toward the end of April. The other two were captured much earlier, on 2 April. Because of their near perfect condition, it is unlikely that they were overwintered butterflies that migrated from Mexico or from other potential overwintering sites in

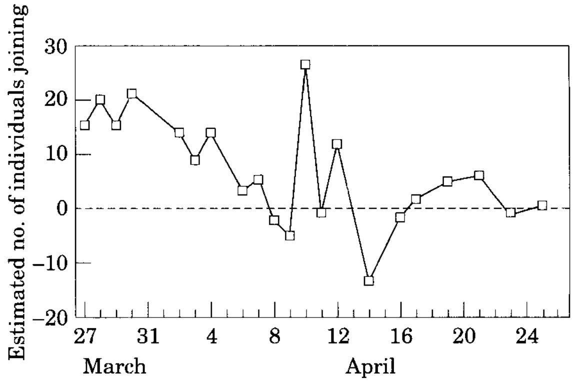

Figure 6. Jolly–Seber estimate of number of individuals joining the Cross Creek monarch population in March–April 1995.

south Florida. Adults newly eclosed by 2 April would have to have been eggs at least three weeks before. Because virtually no *A. humistrata* plants had come up by mid-March at Cross Creek, a more likely explanation is that these two individuals were offspring of remigrants that arrived during mid-March further south in Florida (Knight and Brower, in prep.). Three of the four new spring generation butterflies were never recaptured.

In 1996, we captured two females that appeared freshly eclosed, one on 19 April and the other on 2 May. Unlike the more worn females that were all mated as determined by abdominal palpation for spermatophores, neither of these individuals had mated. We did not detect a second wave of egg-laying in 1995 or 1996. By early June in both years, all the adults had disappeared and the *A. humistrata* plants were senescing.

DISCUSSION

The main objective of our study was to determine the manner in which remigrant monarch butterflies from Mexico establish their first spring generation in the southeastern U.S.A. To do this, we quantitatively estimated population size and residence time of remigrants as they established a breeding population in north-central Florida in the spring of 1995. We also determined the number of waves of incoming monarchs and made comparisons of relative population sizes among three years, from 1994 to 1996.

Residence time in the migratory Cross Creek population

Although the populational origins and the biological conditions affecting monarchs in Australia differ from those in eastern North America and may confound direct comparisons between the two populations, doing so is nevertheless interesting. In Australia both monarchs and their milkweed host plants became naturalized during the 19th century and co-occur mainly along the eastern coast where the exotic milkweeds, intolerant of dry conditions and frost, are able to survive in large patches (James, 1993). Additionally, only one of the milkweed species (*A. curassavica*) is of New World origin, while the other three (two in the genus *Gomphocarpus* and one in the genus *Calotropis*) originated in tropical Africa where the monarch does not occur. Southeastern Australia also has much milder winters than the area occupied by the eastern migratory monarch population in North America, allowing the butterflies to breed year round (Zalucki, 1993). In contrast, *A. humistrata* in north central Florida rapidly senesces as the spring advances and the plants have a scattered distribution which must force the monarchs to keep moving in order to find new hostplants.

Most of the monarchs arriving at Cross Creek remained from 4 to 6 days on average (Table 3). This is much shorter than their expected remaining lifespan. Our findings, combined with the known lifespan of 40 days for reproductively active monarchs in captivity (Zalucki, 1981), suggest that the remaining lifespan of individuals returning to Cross Creek is potentially 20–30 days. In fact, our data determined that several individuals stayed and survived at Cross Creek for more than 20 days. Thus, our mean residence estimate of 4–6 days almost certainly represents short average residence time rather than short longevity. Based on a 5–10 months study in which milkweed patches were sampled weekly in Queensland, Australia, Zalucki and Kitching (1984) found that monarchs survived for several weeks in a milkweed patch, with an estimated mean of 12.4 days compared to our Cross Creek mean minimum lifespan estimate of 6.15 days. We think that the difference in the two studies reflects their resident *versus* our migratory population.

Thin layer chromatography (TLC) fingerprint data indicated that at least two-thirds of Cross Creek monarchs had fed as larvae on the northern milkweed, *A. syriaca* (Knight, 1998). Since this milkweed does not naturally occur south of Virginia, our Cross Creek monarchs had to have been individuals that bred in the northern U.S.A. and southern Canada the previous summer, then migrated southward to central Mexico in the autumn, and then migrated northward to Cross Creek the following spring. The Cross Creek individuals were therefore at least 7 months old and it might be expected that they would disappear rapidly from the population due to death. However, as discussed below and in Knight (1998), we found that the wing condition of most initially captured monarchs was good and, especially in the first half of the study period, very few individuals had tattered or worn wings (Fig. 4). This slow aging strongly suggests that emigration is the most likely explanation for individuals disappearing from the Cross Creek population and provides additional support for our hypothesis of short residence time rather than rapid senescence and mortality in the milkweed patch. In fact, we never found any dead adults during the 3 years of the study.

We thus interpret the short mean residence of Cross Creek monarchs as strong evidence that they are transitory and that the population overall is continuing to migrate. Residence time was variable, however, ranging from 1 to 26 days, which suggests the possibility of a facultative response to host plants along the migratory routes.

The changes in mean residence time over the study period coincide with the phenology of the host plants at Cross Creek. During the last week of March, when the mean residence was approximately 4 days, the milkweeds were newly sprouted and in good condition. By the first week of April, when mean residence was almost 7 days, the milkweeds were at their peak numbers, and most were in the bud or flower stage. We have repeatedly observed that females prefer to oviposit on tender new leaves, flowers and buds. Juvenile monarchs that spend approximately 2–3 weeks developing on the hostplant can encounter dry, tough, or even dead plant parts if the milkweed is too far into its cycle when the eggs are laid. During mid-late April, when residence time dropped off sharply to 2–3 days, most milkweeds were past flowering and were becoming senescent. The declining quality of larval food, the paucity of nectar sources and the decrease in remaining lifespan for adults likely all contribute to the shorter residence time toward the end of our study.

Comparison of residence times for males and females

As Zalucki (1993) pointed out, individuals may leave or stay in a milkweed patch, and the reasons they do so may differ for males and females. Three different methods of analyzing our data indicated that residence time was longer for females than males at Cross Creek (Table 3). In contrast, Zalucki and Kitching (1984) found that in Queensland, males were resident in milkweed patches longer than females, and that females tended to leave patches where male density was low. This also was shown by male removal in very dense *Gomphocarpus* patches (Bull *et al.*, 1985; Suzuki & Zalucki, 1986). Zalucki (1993) suggested that, when females are sexually mature, they are attracted to a milkweed patch both for oviposition and by the frequency with which they encounter males. He also held that the females are repulsed from milkweed patches after mating and disperse to avoid more sexual encounters. Shapiro (1970) had earlier proposed that female Pierid butterflies also emigrate to avoid sexual interactions.

Although avoidance of males may play a role in female emigration, it does not seem the most likely explanation for our Cross Creek population. Here females in fact were less likely to emigrate than males, and, for most of the season, the estimated sex-ratio was female biased (Fig. 5A). Moreover, most females captured there in past years were multiply mated (Knight, unpublished data). We therefore conclude that oviposition sites, rather than mating partners, appear to be the primary attraction for females in the eastern North American monarch population. Sandhill milkweeds, i.e. oviposition sites, were abundant at Cross Creek, and this may have encouraged females to stay and continue ovipositing. The time required for a female to lay her eggs depends on her remaining fecundity which, in turn, depends on her age, the number of eggs she has previously laid, and the number and quality of spermatophores she received in mating (Munger & Harriss, 1970; Zalucki, 1981; Oberhauser, 1989). On the other hand, too many females could overpopulate the plants and possibly trigger female emigration.

Evolutionarily, females are the primary resource for males. Because last-male sperm displacement is common in monarchs (Oberhauser, pers. comm.), it is advantageous for males to continue migrating with the females and for them to copulate with as many females as possible. Thus, when the sex ratio is female-biased in a milkweed patch, males should not emigrate.

So why is residence time for males shorter than for females at Cross Creek? One explanation could be that aggressive male–male interactions force some males to leave the site. The aggressive behaviour of territorial male swallowtail butterflies has been shown to increase the dispersal of 'new' males (Lederhouse, 1983). In monarchs, male–male encounters often lead to fast, high, erratic flight by one or both males which could result in emigration from a site (Pliske, 1975; Zalucki, 1993). Females

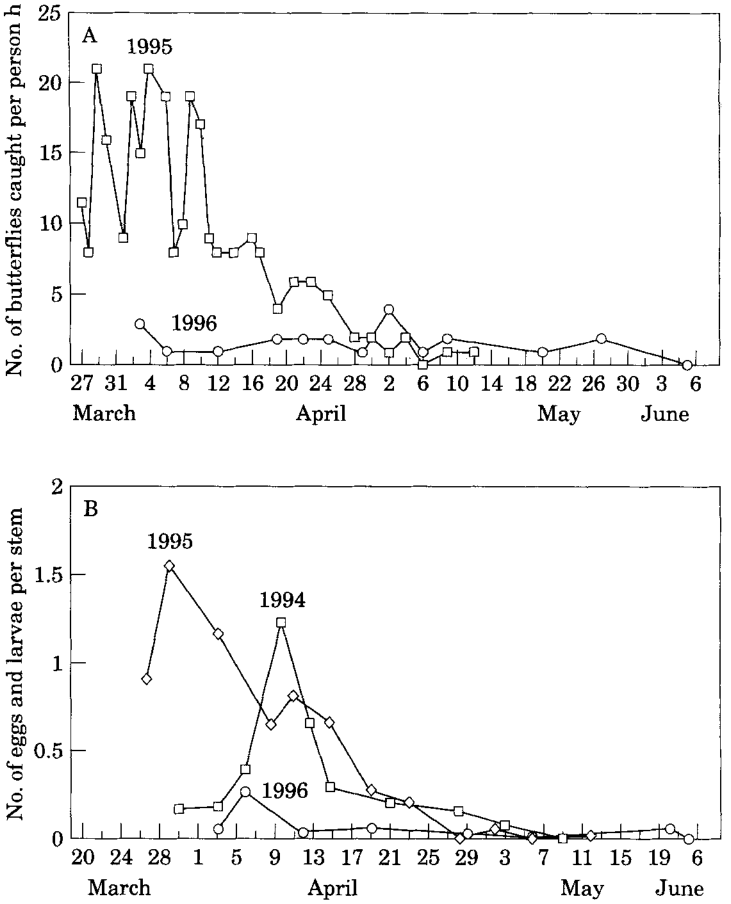

Figure 7. Yearly comparison of the population size of Cross Creek monarchs by two indices over three years: (A) the number of adults caught per person hour in 1995 and 1996; and (B) the number of eggs and larvae per stem in 1994, 1995, and 1996.

may also display the same response after being pursued by a male in an unsuccessful mating attempt. More information is needed on the frequency and results of male–male and male–female encounters to determine if these behaviours, and therefore the local monarch population size in milkweed patches, could differentially affect male and female residence times.

The difference could also be explained by mortality differences. Although we assume that most individuals disappeared from the population due to emigration, mortality undoubtedly accounted for some of the losses. Watt *et al.* (1977) speculated that shorter residence of female *Colias* was caused by higher predation rates upon them. Females were thought to be more vulnerable during their longer warm-up period and during oviposition when they were close to the ground and concealed in vegetation. At the monarch overwintering sites in Mexico, predatory mice ate larger numbers of male than female monarchs in experimental feeding trials (Glendinning, 1993). Similarly, Alonso-Mejia (1996) found that predatory grosbeaks killed a significantly higher number of males than females. Similar findings were attributed to lower cardenolide concentrations in males (Brower & Calvert, 1985) and the abilities of some mouse and bird predators to discriminate palatable butterflies based on taste (Fink & Brower, 1981; Brower, 1988; Glendinning *et al.*, 1990; Glendinning, 1993). Taste discrimination by predators probably is an evolutionary response to the superabundance of monarchs at the overwintering sites. However, it seems unlikely that taste discriminating predators played a significant role in mortality of males at Cross Creek, and we have never seen monarchs pursued by birds at this site (L. Brower, pers. observ. 1981–1996).

Another potential explanation for higher mortality rates of males is faster aging. Mating may be costly to males that produce spermatophores up to 10% of their body mass (Oberhauser, 1988, 1989). Males also expend substantial energy patrolling for females; they chase most things that move including other males and other butterfly species. The expense of previous summer and early winter matings has been hypothesized to explain male-biased sex ratios late in the overwintering period in California (Van Hook, 1996), where males deteriorate faster than females due to their frenzied courtship behaviour (Tuskes & Brower, 1978). This appears to result in their 'burning out', so that a large percentage of males do not leave the California overwintering sites (Hill *et al.*, 1976). Our Cross Creek data suggest that nearly equal numbers of the two sexes leave their overwintering sites in Mexico (see also Malcolm *et al.*, 1993). It seems likely that energy lost through courtship and spermatophore transfer along the migration routes and in the milkweed patches may contribute to their more rapid aging, and thus apparent higher mortality, during the spring remigration.

Arrival time and milkweed phenology in north-central Florida

Arrival times of monarchs at Cross Creek vary from year to year, but in general they coincide with those of remigrants in the more westerly Gulf Coast states. Thus over a 6 year period from 1983 to 1988, Riley (1993) observed monarchs arriving consistently in Louisiana during the last week of March through mid-April. While photoperiod and temperature determine when monarchs are ready to leave Mexico, local weather conditions may trigger their departure and influence their arrival dates in north-central Florida. The butterflies may also use tailwinds associated with fronts to facilitate their long distance migration (Gibo & Pallett, 1979; Schmidt-Koenig, 1985; Brower, 1996). Tracking spring weather fronts along the Gulf Coast moving north in Mexico and eastward in the U.S.A. may contribute to a more accurate prediction of arrival times of the spring remigrants.

The cues monarchs use to leave their overwintering sites in Mexico are well timed to allow maximum exploitation of *A. humistrata* in north-central Florida. The monarch population reached its maximum size in the second week of April following two apparent influxes (Fig. 3) and after mid-April it rapidly declined and disappeared. By this time most of the milkweeds were past flowering with dry or tough leaves, which, as argued above, probably explains the higher emigration rates later in the season. If monarchs arrive much earlier than 1 April, the milkweeds would be just emerging from the ground, and the new leaves are subject to being killed by frost. We have observed frosted *A. humistrata* plants over several years in north-central Florida, including March 1996 (Brower, unpublished observations).

Population trends among years

The monarch population at Cross Creek in 1996 was only about one ninth of what it was in 1995. Weather may play a role in determining the sizes of the remigrating populations. Strong westerly winds associated with frontal systems may cause some monarchs to get blown as far east as north-central Florida. Brower (1996) reviewed the evidence suggesting that migrating monarchs are able to compensate for wind drift. In some cases compensation may not be strong enough, and the butterflies may get blown off course. For example, during the fall migration, monarchs regularly arrive in Bermuda, 1040 km east of Cape Hatteras, in September and October (Urquhart & Urquhart, 1976; Brower, 1995). Unusual movements of spring weather systems predominantly northward or westward could result in very few remigrants making it to Florida, and, therefore to the Cross Creek study site.

There is evidence from radar data taken on bird migration that this happened in the spring of 1996 (Brower, 1999). Many neotropical migrant warblers were displaced more than 1000 miles to the west of their normal routes from the Mississippi River valley eastward to the Atlantic coast. In general, peak arrival times for eastern birds and monarchs in the spring are similar, and both migrate in association with weather fronts (Kerlinger *et al.*, 1985). Thus, wind displacement in the spring of 1996 may well have caused the arrival of only small numbers both of monarchs and birds in the east.

Production of the new spring generation

Malcolm *et al.* (1987) reported two peaks in egg-laying along the roadsides near our Cross Creek study area in 1983, one in early April and the other in mid-June. They interpreted these findings as indicating the production of two spring generations. It is likely, however, that the second wave of egg-laying in 1983 was an artifact resulting from roadside mowing where the egg censuses were made. As noted above, by mid-May most sandhill milkweeds in North Florida are past flowering and have tough, dry leaves that are increasingly unsuitable for oviposition. In 1995 and 1996 we found no evidence for two generations. The natural phenology of *A. humistrata* in our pasture supports the hypothesis that only one monarch generation is normally produced on this milkweed in north-central Florida, and our data argue that the freshly hatching butterflies of the new generation continue the migration northward almost immediately after they emerge from their chrysalids.

Catchability

Determining relative catchability among all members of a population is important both for validating the mark-recapture population estimators and for understanding behavioural differences among potential subgroups within a population, including the two sexes. Greater apparency of males has led to strong male biased capture frequency in many mark-recapture studies of butterflies (Brussard & Ehrlich, 1970; Ehrlich & Gilbert, 1973; Scott, 1973; Tabashnik, 1980; Lederhouse, 1982, 1983; Tabashnik *et al.*, 1992). The higher percentage of male recaptures in Table 2 and the capture ratio *vs.* estimated sex ratio test (Tabashnik, 1980) suggested that males may have been more easily captured than females in our 1995 study, but the joint residence-catchability test indicates that the difference was not statistically significant.

The behaviour of males and females as it relates to catchability is biologically interesting. We observed that the males spent most of their time patrolling the pasture for females, were highly mobile and conspicuous, landed infrequently on vegetation to bask or drink nectar, and were difficult to net. Females, on the other hand, flew from milkweed to milkweed on which they landed frequently and were not easily distracted from ovipositing. The fact that males were more easily detected than females, but physically more difficult to catch, suggests that the catchability of males and females was 'balanced out' by these behavioural differences and our collection procedure.

CONCLUSIONS AND EVOLUTIONARY IMPLICATIONS

Our study is the first population census that attempts to investigate the strategies that spring monarchs remigrating from the Mexico overwintering sites use to recolonize milkweed host plants in the southeastern U.S.A. Monarchs began arriving in north-central Florida in late March in 1995, and we detected at least two waves of new arrivals, the first at the end of March and the second approximately two weeks later in mid-April. The population declined sharply after mid-April and disappeared by the end of the month. After arriving, adults remained for 4–6 days before continuing their migration, with females remaining on average 1 day longer than males. The finding that monarchs keep migrating raises the perennial question of how far north they actually fly (Brower, 1995).

Arrival times varied among three consecutive years, but all were within the two week window from the last week of March to the first week of April, when fresh *A. humistrata* milkweeds were abundant and the risk of frost had largely passed. There was a ninefold drop in monarch numbers from 1995 to 1996.

Our findings raise many possibilities for future research. An important next step is to continue mark-recapture studies on remigrating adult monarchs to assess yearly variation in population parameters including arrival time, population size, the number of annual waves, and residence time. We attempted this again in 1996, but adult numbers were too low for a Jolly–Seber analysis. An alternative to this intensive mark-recapture procedure is the transect method used by Pollard (1977) and Pollard & Yates (1993), which gives information about seasonal, as well as year-to-year population trends.

Standardized monitoring of monarch populations is being carried out in summer breeding areas, during the fall migration, and at overwintering colonies in Mexico (summary in Walton & Brower, 1996). These are useful for detecting fluctuations in numbers and identifying factors critical to protecting monarch buttefly migration, which has become an endangered biological phenomenon in eastern North America because of deforestation of the overwintering habitat in Mexico (Brower & Malcolm, 1991). The size and arrival time of the spring remigrating monarchs may well be a key indicator of conditions at the overwintering sites. Brower (in press) has predicted that the deterioration of the high elevation forests in Mexico due to lumbering is causing the monarchs to desiccate which induces them to leave sooner and thus arrive prematurely in the southeastern U.S.A. before the danger of frost has past.

It has been argued that the bird-like migration of the monarch butterfly in North America coevolved with the adaptive radiation and northward expansion of the milkweed (*Asclepias*) flora beginning in the Miocene (Woodson, 1954; Young, 1982; Brower, 1985). Brower (1996) also presented evidence that monarchs are migratory throughout their annual cycle of three to five generations.

Our findings at Cross Creek are consistent with these hypotheses. The seven to eight-month-old butterflies returning from Mexico opportunistically locate freshly sprouting milkweeds during the early spring in the southern states. By lingering for only a short time at each milkweed patch they encounter, these old monarchs locate the resurgent milkweed flora over an extensive area in the southern states. Then, within less than a month, their fresh offspring continue the migration and exploit the unfolding cornucopia of milkweeds as the spring advances northward. The more we discover about the biology of this insect, the more remarkable is its annual migratory, breeding and overwintering cycle.

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REFERENCES

Ackery PR, Vane-Wright RI. 1984. *Milkweed butterflies: their cladistics and biology.* Ithaca: Cornell University Press.

Alonso-Mejia A. 1996. Biology and conservation of overwintering monarch butterflies in Mexico. Ph.D. dissertation, University of Florida.

Anderson, JB, Brower LP. 1996. Freeze-protection of overwintering monarch butterflies in Mexico: critical role of the forest as a blanket and an umbrella. *Ecological Entomology* **21:** 107–116.

Barker JF, Herman WS. 1973. On the neuroendocrinology of reproduction in the monarch butterfly. *Journal of Experimental Zoology* **183:** 1–9.

Begon M. 1979. *Investigating Animal Abundance: Capture-Recapture for Biologists.* Baltimore: University Park Press.

Bell CR, Taylor BJ. 1982. *Florida wild flowers and roadside plants.* Chapel Hill, NC: Laurel Hill Press.

Brower LP. 1985. New perspectives on the migration biology of the monarch butterfly, *Danaus plexippus* L. In: Rankin MA, ed. *Migration: mechanisms and adaptive significance.* Austin, Texas: University of Texas, 748–785.

Brower LP. 1988. Avian predation on the monarch butterfly and its implications for mimicry theory. In: Brower LP, ed. *Mimicry and the evolutionary process* Chicago: University of Chicago Press, 4–6.

Brower LP. 1995. Understanding and misunderstanding the migration of the monarch butterfly (Nymphalidae) in North America: 1857–1995. *Journal of the Lepidopterists' Society* **49:** 304–385.

Brower LP. 1996. Monarch butterfly orientation: missing pieces of a magnificent puzzle. *Journal of Experimental Biology* **199:** 93–103.

Brower LP. 1999. Oyamel forest ecosystem conservation in Mexico is necessary to prevent the extinction of the migratory phenomenon of the monarch butterfly in North America. In: Canevari P. ed. *Endangered Migrations in the World.* Bonn, Germany: International Union for the Conservation of Nature (IUCN publication), 41–50.

Brower LP. In press. Biological necessities for monarch butterfly overwintering in relation to the Oyamel forest ecosystem in Mexico. In: Pisanty I, Price S, Merino, L., Hoth J, Wilkinson T, Oberhauser K, eds. *Symposium on the Conservation of the Monarch Butterfly.* Morelia, Mexico (November 1997),

Brower LP, Calvert WH. 1985. Foraging dynamics of bird predators on overwintering monarch butterflies in Mexico. *Evolution* **39:** 852–868.

Brower LP, Calvert WH. 1986. The location of monarch butterfly (*Danaus plexippus* L.) overwintering colonies in Mexico in relation to topography and climate. *Journal of the Lepidopterists' Society* **40:** 164–187.

Brower LP, Malcolm SB. 1991. Animal migrations: endangered phenomena. *American Zoologist* **31:** 265–276.

Brussard PF, Ehrlich PR. 1970. The population structure of *Erebia epipsodea* (Lepidoptera: Satyrinae). *Ecology* **51:** 119–129.

Bull CM, Zalucki MP, Suzuki Y, Mackay DA, Kitching RL. 1985. An experimental investigation of patch use by female monarch butterflies, *Danaus plexippus* (L.). *Australian Journal of Ecology* **10:** 391–398.

Clewell AF. 1985. *Guide to the vascular plants of the Florida panhandle.* Tallahassee: Florida State University Press.

Cockrell BJ, Malcolm SB, Brower LP. 1993. Time, temperature, and latitudinal constraints on the annual recolonization of eastern North America by the monarch butterfly. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 233–251.

Cohen JA, Brower LP. 1982. Oviposition and larval success of wild monarch butterflies (Lepidoptera: Danaidae) in relation to host plant size and cardenolide concentration. *Journal of the Kansas Entomological Society* **55:** 343–348.

Cook LM, Brower LP, Croze HJ. 1967. The accuracy of a population estimation from multiple recapture data. *Journal of Animal Ecology* **36:** 57–60.

Cormack RM. 1966. A test for equal catchability. *Biometrika* **22:** 330–342.

Deevey ES. 1947. Life tables for natural populations of animals. *Quarterly Review of Biology* **22:** 283–314.

Ehrlich PR, Gilbert LE. 1973. Population structure and dynamics of the tropical butterfly *Heliconius ethilla. Biotropica* **5:** 69–82.

Fales JH. 1984. Spring occurrence of the monarch butterfly in Maryland. *Maryland Entomologist* **2:** 76–79.

Fink LS, Brower LP. 1981. Birds can overcome the cardenolide defence of monarch butterflies in Mexico. *Nature* **291:** 67–70.

Gibo DL, Pallett MJ. 1979. Soaring flight of monarch butterflies, *Danaus plexippus* (Lepidoptera: Danaidae), during the late summer migration in southern Ontario. *Canadian Journal of Zoology* **57:** 1393–1401.

Glendinning JI. 1993. Comparative feeding responses of the mice *Peromyscus melanotis, P. aztecus, Reithrodontomys sumichrasti,* and *Microtus mexicanus* to overwintering monarch butterflies in Mexico. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 323–334.

Glendinning JI, Brower LP, Montgomery CA. 1990. Responses of three mouse species to deterrent chemicals in the monarch butterfly. I. Taste and toxicity tests with artificial diets laced with digitoxin or monocrotaline. *Chemoecology* **1:** 114–123.

Haber WA. 1993. Seasonal migration of monarchs and other butterflies in Costa Rica. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 201–208.

Herman WS. 1973. The endocrine basis of reproductive inactivity in monarch butterflies overwintering in central California. *Journal of Insect Physiology* **19:** 1883–1887.

Herman WS. 1981. Studies on the adult reproductive diapause of the monarch butterfly. *Biological Bulletin* **160:** 89–106.

Herman WS. 1986. Hormonally mediated events in adult monarch butterflies. In: Rankin MA, ed. *Migration: mechanisms and adaptive significance.* Austin, Texas: University of Texas Contributions in Marine Science, 800–815.

Herman WS. Brower LP, Calvert WH. 1989. Reproductive tract development in monarch butterflies overwintering in California and Mexico. *Journal of the Lepidopterists' Society* **43:** 50–58.

Hill FHJ, Wenner AM, Wells PH. 1976. Reproductive behaviour in an overwintering aggregation of monarch butterflies. *American Midland Naturalist* **95:** 10–19.

James DG. 1993. Migration biology of monarchs in Australia. In: Malcolom SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 189–200.

Janzen DH. 1983. Insects: Introduction. In: Janzen DH, ed. *Costa Rican natural history.* Chicago: University of Chicago Press, 619–645.

Jolly GM. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* **52:** 225–244.

Kerlinger P, Bingham VP, Able KP. 1985. Comparative flight behaviour of migrating hawks studied with radar tracking during autumn in central New York. *Canadian Journal of Zoology* **63:** 755–761.

Knight A. 1998. A Population study of monarch butterflies in North-central and South Florida. *M.S. Thesis.* University of Florida.

Krebs CJ. 1989. *Ecological methodology.* New York: Harper & Row.

Krebs CJ. 1994. *Ecology: the experimental analysis of distribution and abundance.* New York: HarperCollins College Publishers.

Krebs CJ. 1995. *Fortran programs for ecological methodology.* Setauket, NY: Exeter Software.

Lederhouse RC. 1982. Factors affecting equal catchability in two swallowtail butterflies, *Papilio polyxenes and P. glaucus. Ecological Entomology* **7:** 379–383.

Lederhouse RC. 1983. Population structure, residency and weather related mortality in the black swallowtail butterfly, *Papilio polyxenes. Oecologia* **59:** 307–311.

Leslie PH, Chitty D. 1951. The estimation of population parameters from data obtained by means of the capture-recapture method. I. The maximum-likelihood equations for estimating the death rate. *Biometrika* **38:** 269–292.

Leslie PH, Chitty D, Chitty H. 1953. The estimation of population parameters from data obtained by means of the capture-recapture method. III. An example of the practical applications of the method. *Biometrika* **40:** 137–169.

Lynch SP, Martin RA. 1993. Milkweed host plant utilization and cardenolide sequestration by monarch butterflies in Louisiana and Texas. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 107–123.

Malcolm SB, Cockrell BJ, Brower LP. 1987. Monarch butterfly voltinism: effects of temperature constraints at different latitudes. *Oikos* **49:** 77–82.

Malcolm SB, Cockrell BJ, Brower LP. 1993. Spring recolonization of eastern North America by the monarch butterfly: successive brood or single sweep migration? In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 253–267.

Moranz R, Brower LP. 1998. Geographic and temporal variation of cardenolide-based chemical defenses of Queen butterfly *(Danaus gilippus) in northern Florida. Journal of Chemical Ecology* **24:** 905–932.

Munger F, Harriss TT. 1970. Laboratory production of the monarch butterfly, *Danaus plexippus. Journal of Research on the Lepidoptera* **8:** 169–176.

Oberhauser KS. 1988. Male monarch butterfly spermatophore mass and mating strategies. *Animal Behaviour* **36:** 1384–1388.

Oberhauser KS. 1989. Effects of spermatophores on male and female monarch butterfly reproductive success. *Behavioral Ecology and Sociobiology* **25:** 237–246.

Pliske TE. 1975. Courtship behaviour of the monarch butterfly, *Danaus plexippus L. Annals of the Entomological Society of America* **68:** 143–151.

Pollard E. 1977. A method for assessing changes in the abundance of butterflies. *Biological Conservation* **12:** 115–134.

Pollard E, Yates TY. 1993. *Monitoring butterflies for ecology and conservation.* London: Chapman and Hall,

Riley TJ. 1993. Spring migration and oviposition of the monarch butterfly, *Danaus plexippus* L., in Louisiana. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 269–273.

Schmidt-Koenig K. 1985. Migration strategies of monarch butterflies. In: Rankin MA, ed. *Migration: mechanisms and adaptive significance.* Austin, Texas 27 (Supplement): University of Texas Contributions in Marine Science, 786–789.

Scott JA. 1973. Convergence of population biology and adult behaviour in two sympatric butterflies, *Neominois ridingsii* (Papilionoidea: Nymphalidae) and *Amblyscirtes simius* (Hesperoidea: Hesperiidae). *Journal of Animal Ecology* **42:** 663–672.

Seber GAF. 1973. *The estimation of animal abundance and related parameters.* London: Griffin.

Shapiro AM. 1970. The role of sexual behaviour in density-related dispersal of Pierid butterflies. *The American Naturalist* **104:** 367–372.

Suzuki Y, Zalucki MP. 1966. The influence of sex ratio on female dispersal in *Danaus plexippus* (L.) (Lepidoptera: Danaidae). *Journal of the Australian Entomological Society* **25:** 31–35.

Tabashnik BE. 1980. Population structure of Pierid butterflies. *Oecologia* **47:** 175–183.

Tabashnik BE, Perreira WD, Strazanac JS, Montgomery SL. 1992. Population ecology of the Kamehameha butterfly (Lepidoptera: Nymphalidae). *Annals of the Entomological Society of America* **85:** 282–285.

Tuskes PM, Brower LP. 1978. Overwintering ecology of the monarch butterfly, *Danaus plexippus L.*, in California. *Ecological Entomology* **3:** 141–153.

Urquhart. 1960. *The monarch butterfly.* Toronto: University of Toronto Press.

Urquhart FA, Urquhart NR. 1976. Migration of butterflies along the Gulf Coast of northern Florida. *Journal of the Lepidopterists' Society* **30:** 59–61.

Van Hook T. 1993. Non-random mating in monarch butterflies overwintering in Mexico. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 49–60.

Van Hook T. 1996. Monarch butterfly mating ecology at a Mexican overwintering site: proximate causes of non-random mating. Ph.D. thesis, University of Florida.

Vane-Wright RI. 1993. The Columbus hypothesis: an explanation for the dramatic 19th century range expansion of the monarch butterfly. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 179–187.

Walton RK, Brower LP. 1996. Monitoring the fall migration of the monarch butterfly *Danaus plexippus* L. (Nymphalidae: Danaidae) in eastern North America 1991–1994. *Journal of the Lepidopterists' Society* **50:** 1–20.

Wassenaar LI, Hobson KA. 1999. Natal origins of migratory monarch butterflies at wintering colonies in Mexico: new isotopic evidence. *Proceedings of the National Academy of Sciences USA* **95:** 15436–15439.

Watt WB, Chew FS, Snyde RLG, Watt AG, Rothschild DE. 1977. Population structure of pierid butterflies I. Numbers and movements of some montane *Colias* species. *Oecologia* **27:** 1–22.

Wells H, Wells PH, Rogers SH. 1993. Is multiple mating an adaptive feature of monarch butterfly winter aggregation? In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 61–68.

Woodson RE. 1954. The North American species of *Asclepias L.*. *Annals of the Missouri Botanical Garden* **41:** 1–211.

Wunderlin RP. 1982. *Guide to the vascular plants of Central Florida.* Tampa: University Presses of Florida.

Young AM. 1982. An evolutionary-ecological model of the evolution of migratory behavior in the monarch butterfly, and its absence in the queen butterfly. *Acta Biotheoretica* **31:** 219–237.

Zalucki MP. 1981. The effects of age and weather on egg laying in *Danaus plexippus* L. (Lepidoptera: Danaidae). *Researches in Population Ecology* **23:** 318–327.

Zalucki MP. 1993. Sex around the milkweed patch- the significance of patches of host plants in monarch reproduction. In: Malcolm SB, Zalucki MP, eds. *Biology and conservation of the monarch butterfly.* Los Angeles: Publications of the Los Angeles County Museum of Natural History, 69–78.

Zalucki MP, Brower LP. 1992. Survival of first instar larvae of *Danaus plexippus* (Lepidoptera: Danainae) in relation to cardiac glycoside and latex content *of Asclepias humistrata* (Asclepiadaceae). *Chemoecology* **3:** 81–93.

Zalucki MP, Kitching RL. 1984. The dynamics of adult *Danaus plexippus* L. (Danaidae) within patches of its food plant, *Asclepias spp. Journal of the Lepidopterists' Society* **38:** 209–219.

Zalucki MP, Suzuki Y. 1987. Milkweed patch quality, adult population structure, and egg laying in the monarch butterfly. *Journal of the Lepidopterists' Society* **41:** 13–22.