MONITORING THE FALL MIGRATION OF THE MONARCH BUTTERFLY *DANAUS PLEXIPPUS* L. (NYMPHALIDAE: DANAINAE) IN EASTERN NORTH AMERICA: 1991–1994

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ABSTRACT. The results of two different sampling methods are presented for summer resident and migrant monarch butterflies, *Danaus plexippus* L. (Nymphalidae: Danainae), in the northeastern region of North America during the period 1991–1994. Estimates of the relative numbers of butterflies obtained by the Xerces/NABA Fourth of July Butterfly Counts and by a newly instituted fall census in Cape May, New Jersey are correlated. Monitoring of the relative annual abundance of monarchs of the eastern population and its predicted decline therefore appears feasible. Our Cape May data, as well as historical records, indicate that the monarch's annual fall migration along the Atlantic Coast is a normal, and not an "aberrant" phenomenon. An alternative migration model, based on avian research, is presented as a possible adaptive explanation for the fall migratory movements of the monarch butterfly along the Atlantic Coast.

Additional key words: censusing, transect methods, Fourth of July Butterfly Counts, migration, Atlantic Coastal Plain, Cape May, New Jersey.

Monarch butterflies, *Danaus plexippus* L., remigrating from Mexico annually colonize large areas of North America east of the Rocky Mountains. Successive broods (Malcolm et al. 1993) move northward as far as southern Canada and the northeastern United States where multiple generations are produced each summer (Cockrell et al. 1993). During late summer and early fall, the year's final generation(s) of monarchs migrate southwestward (Urquhart 1960), with survivors ultimately reaching the overwintering sites in the Transverse Neovolcanic Belt of mountains in central Mexico (Urquhart 1976, Urquhart & Urquhart 1976, Brower 1977, 1985, Brower et al. 1977).

Although the monarch is a well studied organism, quantitative data

are lacking on its fall movements, including such basic factors as the phenology and the relative sizes of the migrations. Subsequent to the discovery of monarch overwintering sites in Mexico, a model for the autumnal movement of the eastern North American monarch population i.e., the population that breeds east of the Rocky Mountains, was proposed by Urquhart & Urquhart (1978, 1979) and Urquhart (1987). One aspect of this model dealt with the subset of monarchs found along the east coast—they maintained that migrants heading south along the Atlantic coast in the fall are largely wind drifted and off course. Urquhart described such migrants as "aberrant" and suggested that they ultimately end up in Bermuda or, via the Yucatan, in Central America (Urquhart 1987:138–143).

In reviewing monarch migration, Brower (1995) addressed the specific issues dealing with monarchs migrating to Bermuda, the Bahamas, and the Yucatan Peninsula and concluded that these are essentially "failures of the fall migration to Mexico." Citing the historical record as well as our studies at Cape May, Brower (1995) hypothesized that most migrants east of the Appalachians either move southwestward through the mountains, or follow the coast south to northern Florida, where they turn westward to follow the Gulf Coast on their way to the Mexican overwintering grounds.

Williams (1930) cited approximately 100 observations of migratory movements in North America, of which more than 25% refer to localities along the Atlantic Coast from Hampton, New Hampshire to Charleston, South Carolina (Williams 1930:141–149). These accounts extend back to the nineteenth century and indicate that southern New Jersey, and Cape May in particular, have long been known as concentration areas for southbound monarchs in the fall. For example, an account from Cape May stated "habitually seen according to Holland" (Williams 1930:149). Hamilton (1885) characterized the September 1885 monarch migration at Brigantine, New Jersey as "almost past belief . . . millions is but feebly expressive . . . miles of them is no exaggeration." Roger Tory Peterson (pers. comm.) recalled from his visits to Cape May in the early 1930s trees so completely covered with monarchs that they were "more orange than green." During the last quarter century, reports by hawk counters from the New Jersey Audubon Society's Cape May Bird Observatory have regularly mentioned substantial monarch flights (P. Dunne, pers. comm.). The collective force of these anecdotal accounts suggests that a fall migration of monarchs along the east coast is a normal, recurrent phenomenon.

The purpose of this paper is to present and evaluate a quantitative methodology for estimating the relative size of the monarch's annual fall migrations. We compare two sets of data obtained over four years, from

1991 through 1994. The first was obtained during the summer breeding seasons by the Xerces/NABA (North American Butterfly Association) Fourth of July Butterfly Counts (4JBCs). The second set of data was obtained during the fall migrations in Cape May, New Jersey using a procedure we developed and describe here.

Our results support the hypothesis that a migration along the Atlantic coast is part of the monarch's normal fall migration. More importantly, the estimates of the relative numbers of butterflies obtained by the two very different methods are significantly correlated. A long term study that combines these two independent estimates should therefore allow us to monitor the relative annual abundance of monarchs of the eastern population.

METHODS

The Fourth of July Butterfly Counts. The 4JBCs, initiated by the Xerces Society and now administrated by NABA, have been held annually since 1975. During the 1991–1994 seasons, the number of counts held throughout North America ranged from 145 to 249 (Opler & Swengel 1992, 1994, Swengel & Opler 1993, 1995). Each 4JBC covers a circular area with a diameter of 15 m (24 km). Participants conduct a one day census of all species of butterflies seen in their count area. The annual census reports include location, date, weather conditions, general habitat descriptions, land use, and notes on unique habitats as well as any significant changes in land use. Observational effort for each census is indicated by the number of observers, the number of field parties, total party hours, and total party miles. Relative abundance data can therefore be calculated as a function of the numbers of butterflies per species seen per party hour.

In her review of the "issues, problems, and opportunities" of the 4JBCs, Swengel (1990) enumerated a variety of potential pitfalls of using the data to analyze fluctuations in population sizes of various butterfly species. She concluded that the monarch, however, "is well-qualified for such a study because it is widespread, abundant, easily identified, and a habitat generalist" (Swengel 1990:398–399). In her original and subsequent analyses of monarch populations on both continent-wide and regional bases, Swengel (1994, 1996) used the mean numbers of monarchs per party hour from several of the counts to compare trends in various North American monarch populations.

We used the 4JBC database to extract the 1991–1994 monarch data for the summer breeding censuses made at the 68 sites listed in Table 1 and mapped in Fig. 1. Our data are thus a subset of the 4JBC censuses for the northeastern region, encompassing the area of the

TABLE 1.   Fourth of July Butterfly Counts listed from north to south by latitude, and secondarily from east to west by longitude. Included are site names, site numbers (Ref), latitude and longitude coordinates (lat.N, long.W), census dates, the number of party hours (ph), the total number of monarchs seen (Dp), and the calculated values for monarchs per party hour (Dp/ph). The calculated means of all the censuses for each year are at the bottom of the table. Data extracted from Opler & Swengel (1992, 1994) and Swengel and Opler (1993, 1995).

Location	Ref	lat.N	long.W	1991			
				Date	ph	Dp	Dp/ph
Compton Co., QU	1	45.20	71.45	11/7	8.00	10	1.25
Parc Du Mont Oxford, QU	2	45.20	72.12	14/7	15.80	34	2.15
Missisiquoi, QU	3	45.08	72.48	—	—	—	—
North Hero, VT	4	44.55	73.09	21/6	5.25	2	0.38
Essex Co., VT	5	44.46	71.44	23/6	7.50	1	0.13
Colchester, VT	6	44.32	73.10	17/7	10.00	35	3.50
Camel's Hump, VT	7	44.26	72.51	1/7	9.00	5	0.56
LaPlatte Marsh, VT	8	44.24	73.14	28/7	4.00	9	2.25
Pinkham Notch, NH	9	44.16	71.15	—	—	—	—
Lake Placid, NY	10	44.15	73.59	—	—	—	—
Ferrisburg E., VT	11	44.13	73.15	14/7	4.00	24	6.00
Ferrisburg W., VT	12	44.13	73.15	15/7	3.00	39	13.00
Elizabethtown, NY	13	44.13	73.36	—	—	—	—
Hiram, ME	14	43.55	70.44	—	—	—	—
West Rutland, VT	15	43.35	73.09	—	—	—	—
Danby, VT	16	43.17	73.00	7/7	6.50	4	0.62
Saratoga Co. Arpt., NY	17	43.03	73.52	—	—	—	—
Antioch, NH	18	42.57	72.16	—	—	—	—
Vischer Ferry, NY	19	42.45	73.49	—	—	—	—
N. Berkshire Co., MA	20	42.37	73.07	—	—	—	—
C. Franklin Co., MA	21	42.34	72.31	17/7	32.50	184	5.66
Concord, MA	22	42.26	71.25	16/7	7.00	52	7.43
C. Berkshire Co., MA	23	42.24	73.15	—	—	—	—
S. Berkshire Co., MA	24	42.09	73.20	—	—	—	—
Lower Pioneer Vy., MA	25	42.08	72.33	21/7	5.20	0	0.00
Foxboro, MA	26	42.05	71.15	—	—	—	—
Salisbury, CT	27	42.00	73.21	—	—	—	—
Cumberland, Rl	28	41.59	71.29	—	—	—	—
Sherman, CT	29	41.51	73.30	17/7	4.50	6	1.33
Storrs, CT	30	41.48	72.14	7/7	6.00	32	5.33
Bristol Co., MA	31	41.38	70.58	21/7	6.00	5	0.83
Rocky Hill, CT	32	41.38	72.39	—	—	—	—
Prudence Island, RI	33	41.37	71.18	—	—	—	—
Voluntown, CT	34	41.35	71.51	—	—	—	—
Stormville, NY	35	41.35	73.45	—	—	—	—
Monticello, NY	36	41.34	74.38	—	—	—	—
Aquidneck Island, RI	37	41.32	71.16	—	—	—	—
Meriden, CT	38	41.32	72.48	—	—	—	—
Great Swamp, RI	39	41.26	71.34	—	—	—	—
E. Fairfield Co., CT	40	41.19	73.12	—	—	—	—
E. Frfld./W. New Hav. Cos., CT	41	41.16	72.55	9/7	4.75	17	3.58
Fairfield Co., CT	42	41.12	73.18	27/7	1.00	1	1.00
N. Westchester Co., NY	43	41.12	73.41	14/7	44.00	230	5.23
Block Island, RI	44	41.10	71.33	—	—	—	—
Westport/Fairfield, CT	45	41.10	73.19	—	—	—	—
Springdale, NJ	46	41.05	74.49	—	—	—	—

TABLE 1. Extended.

1992				1993				1994			
Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph
11/7	11.00	0	0.00	—	—	—	—	3/7	10.00	0	0.00
12/7	9.50	0	0.00	—	—	—	—	—	—	—	—
23/8	5.25	0	0.00	—	—	—	—	—	—	—	—
14/6	10.00	0	0.00	13/6	8.25	2	0.24	—	—	—	—
—	—	—	—	23/6	5.00	0	0.00	—	—	—	—
13/7	9.50	1	0.11	18/7	7.00	1	0.14	—	—	—	—
5/7	4.75	0	0.00	5/7	5.50	0	0.00	—	—	—	—
19/7	2.50	0	0.00	4/7	3.00	0	0.00	—	—	—	—
—	—	—	—	—	—	—	—	20/7	5.60	1	0.18
—	—	—	—	—	—	—	—	10/7	6.50	5	0.77
18/7	3.00	0	0.00	—	—	—	—	—	—	—	—
7/7	3.00	0	0.00	8/7	7.00	1	0.14	1/7	6.00	3	0.50
—	—	—	—	14/6	6.50	0	0.00	2/7	9.00	17	1.89
19/7	10.25	0	0.00	17/7	4.50	1	0.22	9/7	5.00	0	0.00
—	—	—	—	—	—	—	—	13/7	6.25	11	1.76
12/7	6.60	1	0.15	—	—	—	—	—	—	—	—
19/7	3.00	0	0.00	—	—	—	—	—	—	—	—
10/7	24.00	11	0.46	—	—	—	—	—	—	—	—
18/7	10.50	0	0.00	4/7	9.75	1	0.10	9/7	8.25	6	0.73
—	—	—	—	26/6	20.00	11	0.55	13/7	22.00	37	1.68
11/7	34.00	3	0.09	10/7	27.00	12	0.44	9/7	38.00	57	1.50
18/7	9.00	1	0.11	10/7	17.50	16	0.91	16/7	19.00	81	4.26
25/7	36.25	6	0.17	—	—	—	—	17/7	21.00	46	2.19
—	—	—	—	10/7	15.00	18	1.20	16/7	18.00	79	4.39
22/7	4.08	2	0.49	—	—	—	—	—	—	—	—
11/7	37.30	9	0.24	11/7	40.00	22	0.55	10/7	45.00	48	1.07
—	—	—	—	—	—	—	—	9/7	18.00	6	0.33
29/7	8.00	0	0.00	—	—	—	—	—	—	—	—
18/7	4.25	0	0.00	—	—	—	—	—	—	—	—
19/7	9.00	2	0.22	13/7	25.50	28	1.10	11/7	27.00	23	0.85
19/7	5.25	0	0.00	18/7	5.00	11	2.20	17/7	5.00	7	1.40
—	—	—	—	—	—	—	—	5/7	8.00	2	0.25
—	—	—	—	—	—	—	—	18/7	7.00	2	0.29
—	—	—	—	—	—	—	—	18/7	6.00	3	0.50
—	—	—	—	20/7	6.50	11	1.69	24/7	8.25	11	1.33
—	—	—	—	—	—	—	—	3/7	5.50	3	0.55
8/7	11.50	1	0.09	—	—	—	—	—	—	—	—
—	—	—	—	17/7	5.50	2	0.36	3/7	5.00	0	0.00
7/7	13.50	0	0.00	—	—	—	—	—	—	—	—
—	—	—	—	3/7	4.00	1	0.25	2/7	6.00	1	0.17
20/7	5.00	0	0.00	1/7	3.00	0	0.00	1/7	4.75	0	0.00
18/7	2.00	0	0.00	31/7	1.50	0	0.00	—	—	—	—
11/7	54.00	24	0.44	10/7	57.00	113	1.98	9/7	54.00	201	3.72
16/7	8.50	10	1.18	—	—	—	—	—	—	—	—
—	—	—	—	17/7	2.50	10	4.00	—	—	—	—
5/7	31.00	2	0.06	11/7	32.00	18	0.56	9/7	24.50	27	1.10

TABLE 1.   Continued.

Location	Ref	lat.N	long.W	1991 Date	ph	Dp	Dp/ph
West Milford, NJ	47	41.05	74.22	28/7	8.00	9	1.13
Long Pond, PA	48	41.03	75.27	—	—	—	—
Greenbrook Sanc., NJ	49	40.54	73.56	20/7	7.00	2	0.29
Brooklyn/Queens Cos., NY	50	40.52	73.54	6/7	24.00	246	10.25
Muttontown, NY	51	40.51	73.32	20/7	33.00	106	3.21
Great Swamp, NJ	52	40.47	74.28	—	—	—	—
Bronx/Manhattan Co., NY	53	40.41	73.51	29/6	27.00	21	0.78
Mariton Wildl. Sanc., PA	54	40.41	75.19	15/6	5.00	2	0.40
Western Suffolk, NY	55	40.40	73.45	30/7	32.00	60	1.88
Staten Island, NY	56	40.35	74.09	22/6	25.00	18	0.72
Hawk Mountain, PA	57	40.35	75.55	—	—	—	—
Pool Wildl. Sanc., PA	58	40.33	75.31	15/6	1.50	0	0.00
Raritan Canal, NJ	59	40.25	74.34	11/7	28.00	126	4.50
Hendricks, PA	60	40.20	75.15	10/8	3.50	14	4.00
Furnace Hills, PA	61	40.13	76.18	—	—	—	—
S. Bucks Co., PA	62	40.11	74.54	—	—	—	—
Bryn Mawr, PA	63	40.02	75.19	15/7	15.00	74	4.93
White Clay Ck., PA	64	39.42	75.45	11/7	5.00	29	5.80
Galloway Township, NJ	65	39.29	74.34	7/7	4.00	9	2.25
Cumberland Co., NJ	66	39.20	75.12	15/6	6.00	34	5.67
Belleplain, NJ	67	39.15	74.56	14/7	32.50	105	3.23
Cape May, NJ	68	39.01	74.52	6/7	37.50	68	1.81
No. Sites and Mean Dp/h				**n = 36**			**3.09**

northern Appalachian Mountains and eastward, including southeastern Quebec, eastern New York and Pennsylvania east to the Atlantic coast, and thence southward through New England to southern New Jersey. Note that site 68 is Cape May, New Jersey where the fall censuses also were made. Table 1 presents the data for the 1991–1994 censuses.

The Cape May Census. Sutton et al. (1991) estimated that 10,106 monarchs passed their lookout at East Point, New Jersey during September through November 1990, with peak flights occurring on 28 September (1,500 monarchs) and 6 October (1,000 monarchs). On 27 September 1990, Walton recorded 618 monarchs moving southwest along the dunes at Cape May Point State Park in one 8-minute period. The following day at the same location the flight averaged 536 monarchs per hour between 0832 h and 1541 h (EST). These informal observations confirmed Cape May Point as having excellent potential for annual monitoring.

Systematic quantitative data collection was initiated at Cape May Point (hereafter called Cape May) during September-October 1991 by Walton and colleagues, under the aegis of the Monarch Migration Association of North America (c/o 7 Concord Greene No. 8, Concord,

TABLE 1. Extended continued.

	1992				1993				1994		
Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph	Date	ph	Dp	Dp/ph
19/7	5.00	1	0.20	27/6	10.00	0	0.00	26/6	16.50	4	0.24
—	—	—	—	—	—	—	—	11/7	6.50	5	0.77
18/7	6.00	0	0.00	17/7	6.00	0	0.00	16/7	6.50	3	0.46
3/7	32.00	3	0.09	5/7	16.00	39	2.44	—	—	—	—
18/7	34.00	50	1.47	17/7	36.00	173	4.81	16/7	37.00	135	3.65
—	—	—	—	—	—	—	—	2/7	26.00	9	0.35
17/6	26.00	1	0.04	26/6	43.00	5	0.12	26/6	22.00	0	0.00
20/6	2.00	0	0.00	23/6	1.50	2	1.33	25/6	1.50	0	0.00
28/6	45.00	0	0.00	3/7	43.00	11	0.26	2/7	52.00	17	0.33
21/7	5.00	0	0.00	18/7	8.00	16	2.00	26/6	8.75	9	1.03
11/7	15.00	0	0.00	3/7	9.50	1	0.11	9/7	17.50	12	0.69
13/6	1.50	0	0.00	19/6	2.00	0	0.00	18/6	2.00	0	0.00
8/7	22.25	0	0.00	15/7	21.25	32	1.51	11/7	18.50	18	0.97
12/8	2.50	0	0.00	—	—	—	—	—	—	—	—
—	—	—	—	26/7	9.25	3	0.32	4/7	9.80	8	0.82
—	—	—	—	26/6	4.00	0	0.00	16/7	9.50	9	0.95
13/7	12.00	0	0.00	28/6	5.00	9	1.80	5/7	6.25	1	0.16
10/7	4.75	0	0.00	—	—	—	—	1/7	6.50	1	0.15
14/7	5.50	4	0.73	18/7	3.50	8	2.29	5/7	5.33	16	3.00
5/7	29.00	6	0.21	27/6	29.00	39	1.34	9/7	28.00	48	1.71
4/7	31.50	3	0.10	26/6	38.00	24	0.63	8/7	33.00	33	1.00
28/6	21.50	4	0.19	18/6	23.00	17	0.74	25/6	38.00	22	0.58
	n = 48		**0.14**		**n = 42**		**0.87**		**n = 47**		**1.03**

Massachusetts 01742, USA); the censusing was continued in the falls of 1992–1994. Based on methods developed by Pollard (1977), data were collected along a census route through a variety of habitats, including southern hardwood forest, agricultural fields, brackish wetland meadow, suburban neighborhoods, and coastal dunes along the Atlantic Ocean and Delaware Bay. While the 1992–1994 route covered a single 8 km transect, the 1991 census employed three shorter transects, albeit of approximately the same total distance and over much of the same ground covered in 1992–1994 (Fig. 2).

Each transect census was made by a single observer driving a car at approximately 32–40 km per hour, with all monarchs counted along the route. No stops were allowed to count specific concentrations of butterflies. Monarch totals, starting and elapsed times, and local weather conditions were recorded during each census. These census data are summarized in Table 2.

Statistical analyses. We used Statview II, version 1.03 (Feldman et al. 1987) to run regression analyses that relate the four annual averages of monarchs seen per census hour at Cape May to the average number of monarchs seen per party hour in the four 4JBC censuses. In these regressions, we defined the Cape May data as the dependent variable,
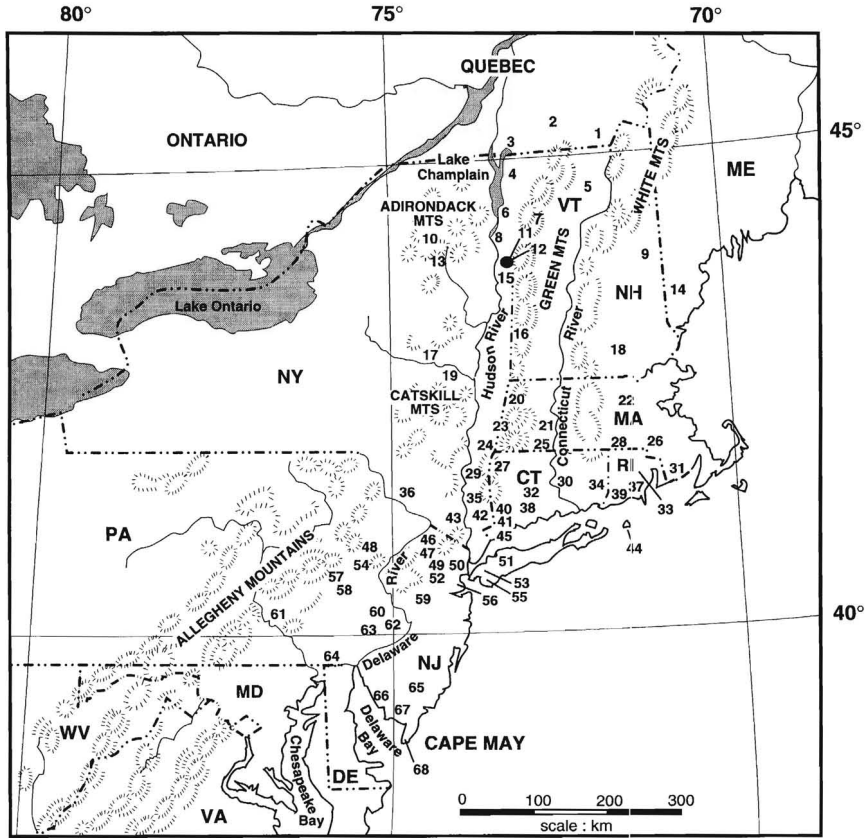
FIG. 1.   Geographic distribution of 68 monarch butterfly census locations of the Fourth of July Butterfly Counts in the northeastern USA, made during the summers of 1991 through 1994. Site 68 is the location of the Cape May road census. See Table 1 for exact locations and yearly census data.

on the rationale that the number of migrants is dependent upon the size of the summer breeding populations.

RESULTS

Table 1 summarizes the 1991–1994 4JBC data for the Northeast in the area from the Appalachian mountain region east through the coastal

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FIG. 2.   Cape May, New Jersey, showing the census routes over the four years. The 8 km route used in 1992–1994 is indicated by arrows. The crosses at the west end of Sunset Boulevard indicate the end of the truncated transect segment traversed in 1991. The base map is reproduced with the permission of P. Sutton of The Cape May Bird Observatory.

—N—

13 miles to
Lewes,
Delaware

START

Ferry Road

Ferry
Terminal

Intracoastal Waterway

Higbee Beach W.M.A

New England Road

*Delaware
Bay*

Pond Creek

Bayshore Road

FINISH

Cape
Ave.

Lighthouse Ave.

Lily
Lake

Cape May
Point
State Park

Migratory
Bird Refuge
(TNC)

Broadway

Sunset Blvd.

**Cape May
Point**

0   1   2

kms

Atlantic Ocean
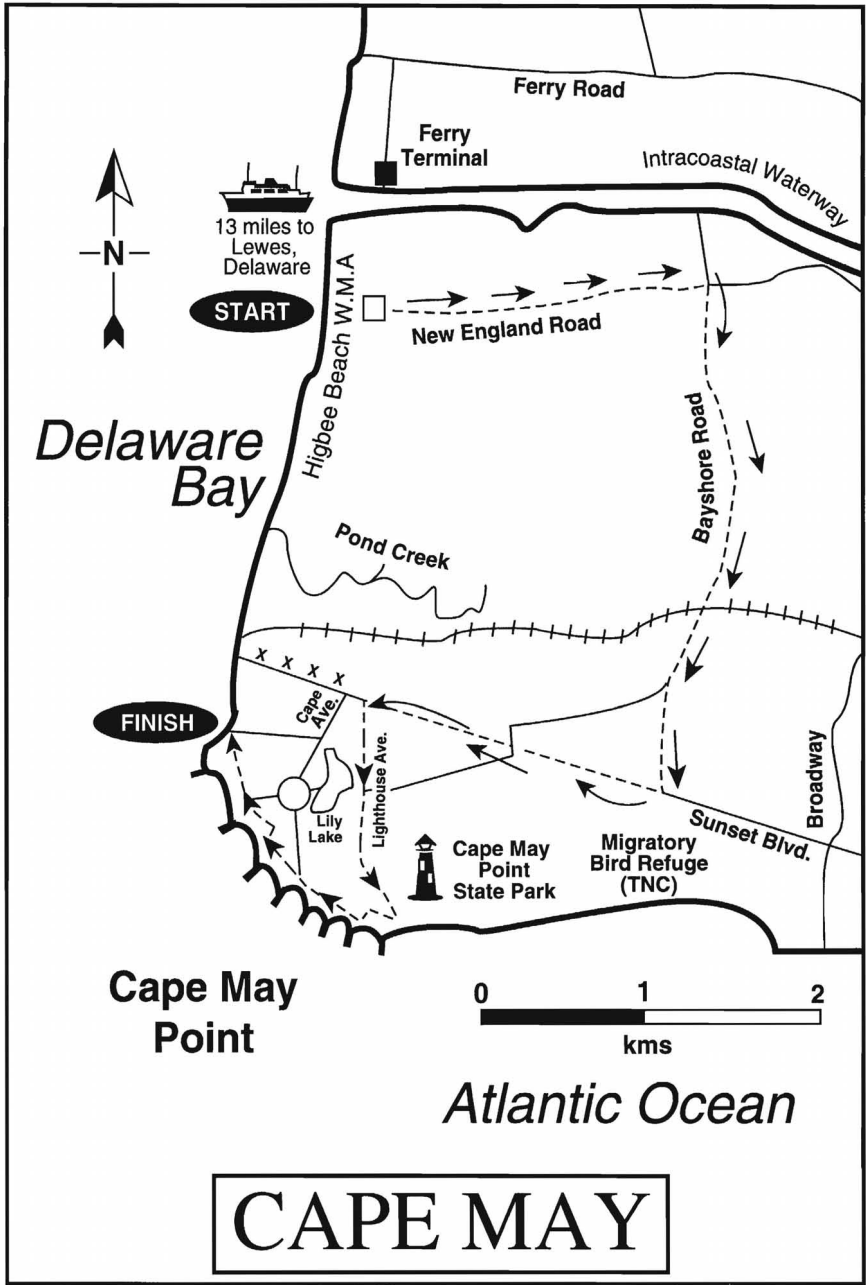
CAPE MAY

TABLE 2. Summary of the 1991-94 Cape May, New Jersey fall monarch migration census data. Included are the census dates, the number of census runs (cr), the total minutes of observation (min), the number of monarchs observed (Dp), and the calculated values for the average number of monarchs seen per census hour per day (Dp/h). The calculated means for the number of monarchs per census hour for each year are at the bottom of the table.

Date	1991				1992				1993				1994			
	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h
1 Sep	—	—	—	—	3	61	16	15.74	3	46	12	15.65	3	52	48	55.38
2 Sep	—	—	—	—	3	56	11	11.79	3	48	9	11.25	3	52	58	66.92
3 Sep	—	—	—	—	3	50	6	7.20	3	48	3	3.75	3	50	19	22.80
4 Sep	—	—	—	—	3	59	9	9.15	3	46	1	1.30	3	51	20	23.53
5 Sep	—	—	—	—	3	58	2	2.07	3	45	13	17.33	3	50	58	69.60
6 Sep	—	—	—	—	3	55	0	0.00	3	48	19	23.75	3	53	229	259.25
7 Sep	—	—	—	—	3	54	6	6.67	3	51	9	10.59	3	52	151	174.23
8 Sep	—	—	—	—	3	58	6	6.21	3	46	8	10.43	3	53	162	183.40
9 Sep	—	—	—	—	3	51	2	2.35	3	17	1	3.53	3	52	119	137.31
10 Sep	—	—	—	—	3	55	6	6.55	3	48	6	7.50	3	52	163	188.08
11 Sep	—	—	—	—	3	62	10	9.68	3	50	13	15.60	3	50	187	224.40
12 Sep	—	—	—	—	3	62	37	35.81	3	59	26	26.44	3	52	200	230.77
13 Sep	—	—	—	—	3	60	23	23.00	3	61	16	15.74	3	53	287	324.91
14 Sep	1	5	14	168.00	3	60	17	17.00	3	63	9	8.57	3	52	185	213.46
15 Sep	1	5	8	96.00	3	53	7	7.92	3	55	17	18.55	3	50	46	55.20
16 Sep	1	5	5	60.00	3	61	7	6.89	3	58	52	53.79	3	50	3	3.60
17 Sep	—	—	—	—	3	55	4	4.36	3	58	79	81.72	3	52	1	1.15
18 Sep	1	5	12	144.00	3	55	5	5.45	3	38	47	74.21	3	55	140	152.73
19 Sep	4	30	34	68.00	3	53	44	49.81	3	61	299	294.10	3	55	456	497.45
20 Sep	2	15	98	392.00	3	54	16	17.78	3	59	153	155.59	3	57	44	46.32
21 Sep	3	20	131	393.00	3	51	8	9.41	1	19	8	25.26	3	55	76	82.91
22 Sep	1	10	109	654.00	3	50	2	2.40	3	57	198	208.42	—	—	—	—
23 Sep	1	10	2	12.00	3	54	21	23.33	3	56	150	160.71	1	18	6	20.00
24 Sep	2	15	46	184.00	3	55	8	8.73	3	53	237	268.30	3	54	75	83.33
25 Sep	—	—	—	—	—	—	—	—	3	54	176	195.56	3	57	27	28.42
26 Sep	1	10	0	0.00	3	56	28	30.00	3	54	71	78.89	—	—	—	—
27 Sep	2	10	3	18.00	3	57	3	3.16	3	34	6	10.59	3	55	11	12.00
28 Sep	2	10	10	60.00	3	53	24	27.17	3	54	92	102.22	3	55	51	55.64
29 Sep	3	20	15	45.00	3	48	1	1.25	3	55	267	291.27	2	35	11	18.86
30 Sep	2	20	18	54.00	3	51	10	11.76	1	19	52	164.21	3	55	203	221.45

TABLE 2. Continued.

Date	1991				1992				1993				1994			
	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h	cr	min	Dp	Dp/h
1 Oct	4	30	5	10.00	3	47	6	7.66	3	51	93	109.41	3	55	222	242.18
2 Oct	1	10	3	18.00	3	47	10	12.77	1	17	17	60.00	3	55	404	440.73
3 Oct	3	20	10	30.00	3	68	12	10.59	2	37	48	77.84	3	56	69	73.93
4 Oct	3	27	11	24.44	3	58	6	6.21	3	54	205	227.78	3	51	20	23.53
5 Oct	5	40	19	28.50	3	54	4	4.44	3	54	37	41.11	2	32	6	11.25
6 Oct	5	40	34	51.00	3	58	4	4.14	3	49	37	45.31	3	46	4	5.22
7 Oct	3	30	96	192.00	3	55	3	3.27	3	50	29	34.80	3	48	11	13.75
8 Oct	5	40	226	339.00	3	58	7	7.24	3	47	67	85.53	3	49	15	18.37
9 Oct	5	40	201	301.50	3	54	2	2.22	3	49	43	52.65	2	35	5	8.57
10 Oct	3	20	22	66.00	3	59	26	26.44	1	17	52	183.53	3	45	3	4.00
11 Oct	4	30	470	940.00	3	54	14	15.56	3	51	27	31.76	3	50	29	34.80
12 Oct	1	10	52	312.00	3	58	38	39.31	—	—	—	—	3	50	21	25.20
13 Oct	—	—	—	—	3	63	55	52.38	2	33	7	12.73	3	47	1	1.28
14 Oct	—	—	—	—	3	61	20	19.67	3	50	11	13.20	2	31	1	1.94
15 Oct	3	20	24	72.00	2	29	9	18.62	3	51	20	23.53	2	31	0	0.00
16 Oct	3	20	8	24.00	2	28	3	6.43	2	35	26	44.57	2	34	19	33.53
17 Oct	—	—	—	—	2	29	4	8.28	1	16	3	11.25	2	33	17	30.91
18 Oct	3	20	25	75.00	2	34	0	0.00	2	32	14	26.25	2	30	6	12.00
19 Oct	3	20	30	90.00	1	14	0	0.00	2	33	5	9.09	2	32	25	46.88
20 Oct	—	—	—	—	2	25	0	0.00	—	—	—	—	2	33	18	32.73
21 Oct	3	20	8	24.00	2	30	0	0.00	2	36	6	10.00	2	33	32	58.18
22 Oct	3	20	2	6.00	2	30	0	0.00	2	34	1	1.76	2	31	10	19.35
23 Oct	3	20	2	6.00	2	28	2	4.29	2	33	7	12.73	—	—	—	—
24 Oct	3	20	6	18.00	2	26	0	0.00	2	32	8	15.00	2	33	42	76.36
25 Oct	—	—	—	—	2	29	1	2.07	2	35	20	34.29	2	33	48	87.27
26 Oct	—	—	—	—	2	28	0	0.00	1	17	5	17.65	—	—	—	—
27 Oct	—	—	—	—	2	28	0	0.00	1	17	6	21.18	2	31	12	23.23
28 Oct	—	—	—	—	2	19	0	0.00	2	32	5	9.38	2	31	12	23.23
29 Oct	—	—	—	—	2	26	0	0.00	2	32	9	16.88	2	31	8	15.48
30 Oct	—	—	—	—	2	30	0	0.00	—	—	—	—	2	30	7	14.00
Mean				**142.20**				**10.40**				**62.90**				**86.30**
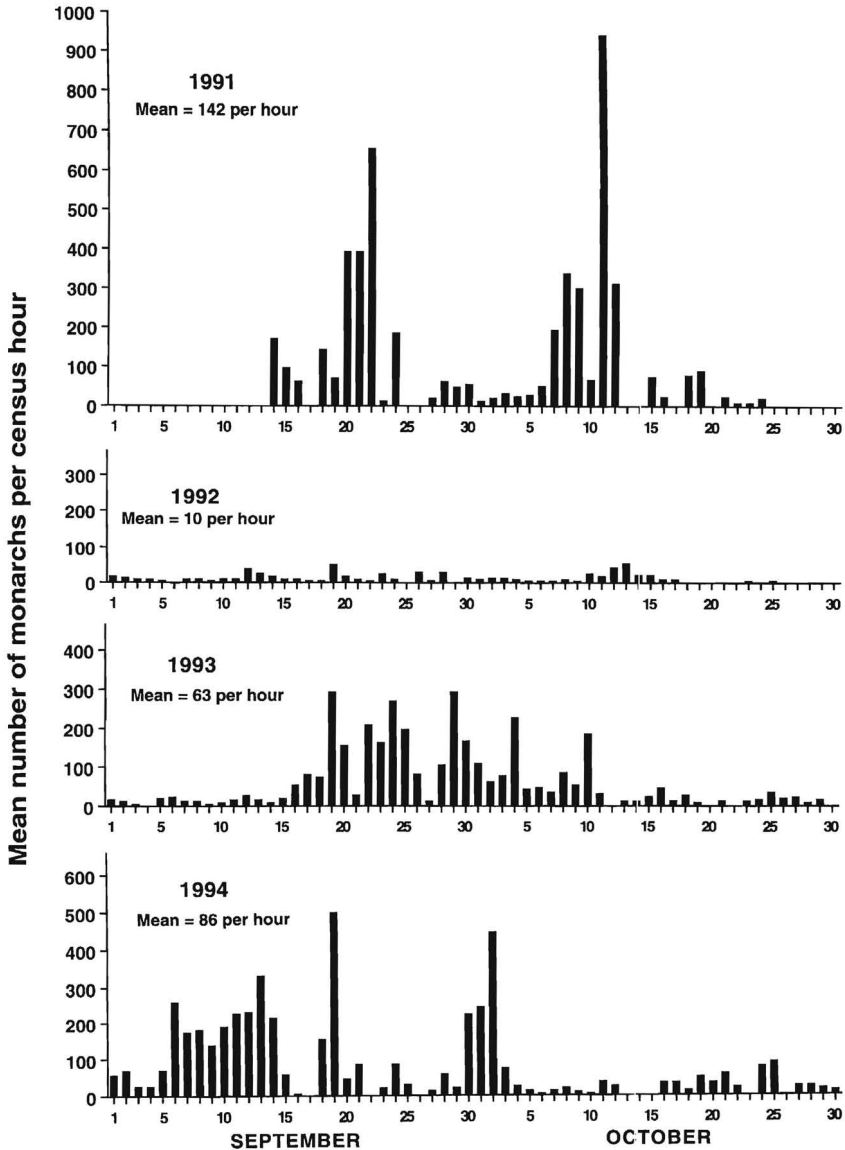
FIG. 3. The daily migration pattern of monarchs along the Atlantic Coast at Cape May, New Jersey during the 1991–1994 fall migrations, based on data in Table 2. Note that: (a) the migration extends over a period of approximately 8 weeks during September and October; (b) there is a greater than fourteen-fold difference in size between the minimum (1992) and maximum (1991) migrations; and (c) there appears to be more than a single pulse of migrant butterflies, which may represent migrants of successive generations (see also Fig. 4). In 1991, no counts were made on 1–13, 17 and 25 September, and on 13, 14, 17, 20, and 25–30 October. Zeros on the 1992–1994 graphs include both

plain. A total of 36 sites reported in 1991, 48 in 1992, 42 in 1993, and 47 in 1994 (Table 1). The calculated figures for the mean numbers of monarchs seen per party hour were: 3.09 for 1991, 0.14 for 1992, 0.87 for 1993, and 1.03 for 1994.

Table 2 summarizes the daily census results at Cape May, New Jersey. During the 1991 season, 93 census runs were conducted between 14 September to 24 October and a total of 1,759 monarchs was counted in 11.5 hours of observation. During the 1992 season, 160 census runs were conducted between 1 September to 30 October and a total of 565 monarchs was counted in 47.2 hours of observation. During the 1993 season, 145 census runs were conducted between 1 September to 30 October and a total of 2,857 monarchs was counted in 40.9 hours of observation. During the 1994 season, 148 census runs were conducted between 1 September to 30 October, and a total of 4,103 monarchs was counted in 42.1 hours of observation. The mean numbers of monarchs per party hour were 142.2 for 1991, 10.4 for 1992, 62.9 for 1993, and 86.3 for 1994.

Figure 3 presents histograms of the daily numbers of monarchs per census hour for each year at Cape May. Because so few monarchs migrated in 1992, Figure 4 shows the same 1992 data on an expanded scale. Figure 5 is a plot of the four seasonal averages obtained by the Cape May censuses (y axis) against the 4JBC censuses (x axis). The regression ($y = 41x + 23$) indicates that the data for the two censuses are significantly correlated ($r^2=0.905$, $F=19.0$, $p=0.049$). We also ran an additional regression that included a hypothetical 0:0 pair of values to the four years' data. It is not unreasonable to do this, because if there were no breeding in the northeastern area, it is likely that there would be virtually no migration through Cape May. This regression ($y = 45x + 14$) was also significant ($r^2=0.913$, $F=31.4$, $p=0.011$).

DISCUSSION

Correlation of the 4JBCs and the Cape May counts. The Fourth of July Butterfly Counts and the Cape May, New Jersey censuses are very different measures of monarch populations in the northeastern region of North America. Besides the methodological differences, the 4JBCs are a measure of the relative size of the summer breeding population, while the Cape May transects are a measure of the migrating population in the fall i.e., the two record different parts of the monarchs'

←

rain days when no censuses were made and days when no monarchs were observed (see Table 2).
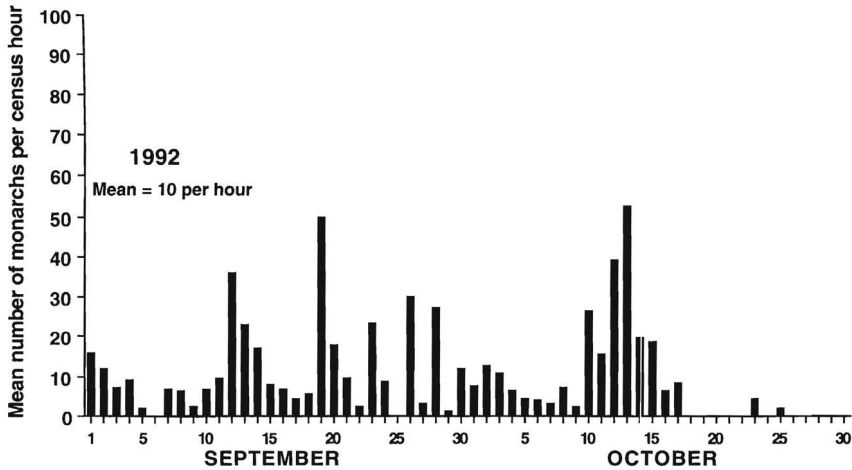
FIG. 4.   The same Cape May, New Jersey data for 1992 as shown in Fig. 3, but scaled up to clarify the phenology of the migration.

annual cycle. We had originally thought that a correlation between the two would at best be weak because of the 4JBC methodologies (Swengel 1990). However, the implication of the significant correlation is that the size of the fall migration along the Atlantic coast can be predicted from the magnitude of the summer breeding population in the northeastern United States. Although more years are needed to confirm this relationship, the data suggest that the 4JBCs and the Cape May census procedures are both valid techniques for estimating the relative size of the monarch population from the Appalachians eastwards.

While our major goal for the Cape May census is to compile at least a ten-year data base, the results of the first 4 years include several additional findings of interest. Of particular note is the major decline in 1992 detected by both measures. This decline corresponds with observations of severe mortality in the Transverse Neovolcanic Belt overwintering sites in Mexico during the preceding winter i.e., in February 1992 (Brower *in* Culotta 1992). Swengel's (1993) summary of all 4JBC data for monarchs east of the Rocky Mountains for 1980–1993 indicated that the summer of 1992 was an average year. Compared to 1991, however, the numbers in the midwestern states were down about 65% in the summer of 1992. If only the northeastern 4JBCs sites are considered (i.e., those in Table 1), the decline from 1991 to 1992 was 95% (= {3.09–0.14/3.09}). This drop closely agrees with our Cape May data, which showed a 93% decline (= {142.16–10.41/142.16}).

Data from both counts in future years should thus continue to provide an annual measure of the regional fluctuations in monarch numbers
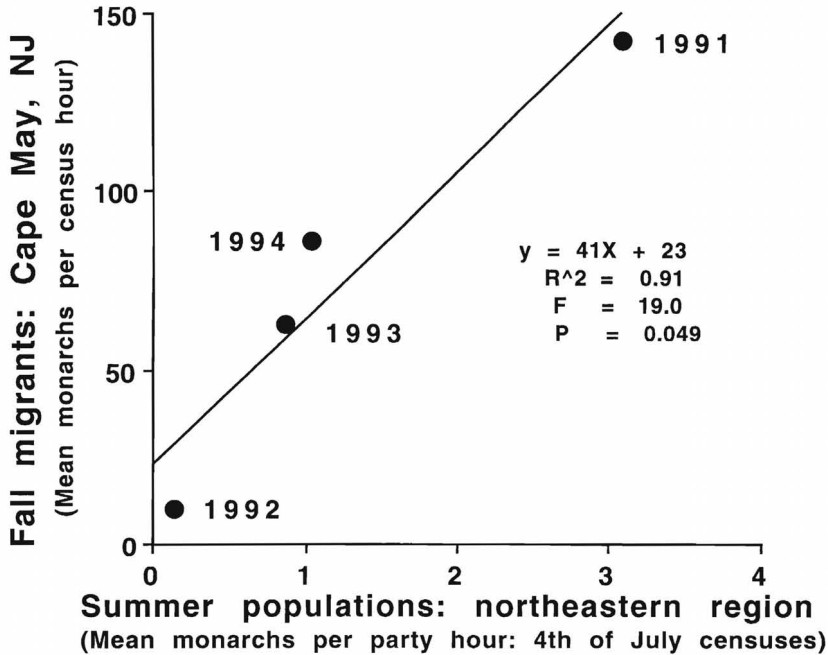
FIG. 5.   Relationship of the yearly means of the 1991–1994 transect censuses made during the fall migration at Cape May, New Jersey and the mean Fourth of July Butterfly Counts made during the summer breeding season for the same four years in the northeastern USA. The Fourth of July Butterfly Count data are from the sampling sites in Fig. 1 and Table 1. The Cape May data are the yearly means of the annual fall migrant census counts from Table 2. The two estimates, made during different seasons and using different methods, are correlated (r^2=0.91) and the regression of the Cape May data on the 4JBC data is statistically significant (F=19.0, p<0.05). The correlation is evidence that both methods are valid estimates of the relative annual abundance of monarchs in the northeastern region, and that the 4JBC estimate of the summer breeding population in the northeast is a good predictor of the relative size of the fall migrant population along the Atlantic coast.

east of the Appalachians, as well as furnishing data for comparison with other regions of the country.

The Atlantic coast migration is not aberrant. During the four-year period of our study we have consistently recorded large numbers of monarchs at Cape May, New Jersey, ranging from 565 to 4,103 individuals (Table 2). We have also regularly observed migratory behaviors including: (1) mass movements along beach and dune lines; (2) a high degree of directionality of monarchs observed both during point counts and during counts of the butterflies crossing Delaware Bay (Walton et al., unpubl. data); (3) roost formations; and (4) significant build-ups and exoduses on consecutive days. Another notable characteristic has been

the timing of the fall movement. In each of the four years studied, the numbers of migrants peaked during the third week of September (Figs. 3–4). A second annual peak also is apparent in 1991, 1992, and 1994.

Our Cape May observations argue in favor of describing the Atlantic coast migrants as routine constituents in the monarch's fall migration. The numbers and behavior of monarchs observed leave little doubt that a significant migration has occurred at Cape May in each year of our censuses. Aspects of the timing of the migration, in particular the recurring September peaks, also indicate a routine passage of monarchs. Such consistent timing of the peaks would be unlikely if they were caused solely by weather conditions such as cold fronts, because the latter do not occur at the same time each year. Finally, the correspondence of the Cape May and 4JBC data sets suggests that the number of monarchs passing through Cape May is representative of northeastern breeding populations as a whole. If this correlation holds in future years, it will strengthen the hypothesis that the Cape May migration is representative of the population of northeastern monarchs, rather than comprising an "aberrant" group displaced by atypical weather conditions, as hypothesized by the Urquharts.

It is instructive to examine briefly the data and inferences that underlie the Urquharts' position. Maps based on release/recapture data (Urquhart & Urquhart 1978, Urquhart 1987) depict their contention that eastern monarchs normally proceed in a southwest direction in fall, directly (more or less) on course to the Mexican wintering grounds. This would, therefore, take most northeastern monarchs on an inland path away from the coast. But their release/recapture data (Urquhart & Urquhart 1978) also indicate that a substantial number of migrants move east—or southeastward and this, they say, can be accounted for by strong westerly and northwesterly winds. Furthermore, they maintained that these "aberrant" monarchs probably end up in locations other than the known wintering sites (Urquhart 1987:141). There is substantial evidence (Gibo 1986, Schmidt-Koenig 1993), including data from the Urquharts (1979), that migrating monarchs are affected by wind drift during migration, and so we consider it unreasonable to conclude that most wind-drifted individuals are necessarily off-course, or that their destination must differ from the main cohort of eastern monarchs. Point to point release/recapture data establish relatively little, if anything, about either the actual tracks taken by individual monarchs or the mean track of the whole migrant population. It seems just as reasonable to hypothesize that large numbers of northeastern monarchs normally move southeastward to the coast and then continue moving southward. In short, we simply do not know what precise course any

individual monarch or group of monarchs takes on its way to the Mexican wintering grounds.

Do hawks and monarchs use a similar migration strategy along the Atlantic coast? Broad-winged hawks, *Buteo platypterus* Vieillot (Accipitridae), are common summer residents of northeastern forests. These hawks overwinter in Central and South America, south to Chile, and considerable research has been done on their migration phenology and flight dynamics (Kerlinger 1989, Dodge 1985–1994). Interestingly, both this hawk and the monarch often are seen migrating together in the fall, and both employ thermal soaring and gliding flight during their migration (Kerlinger 1989, Gibo & Pallett 1978).

One model for the migration of the broad-winged hawk, given by Kerlinger et al. (1985), suggests elliptical migration paths. Such routes would allow these hawks to take advantage of prevailing westerly winds in the northern latitudes of North America, and then the prevailing easterly winds in the southern latitudes. Kerlinger et al. (1985) hypothesize that this would result in a quicker and more energetically efficient departure from the northern portion of their range to the region of 35°N (the approximate latitude of Cape Hatteras, North Carolina on the east coast), where the hawks then could begin to take advantage of the prevailing easterlies. Monarchs may employ a similar strategy, and thus *initially* move eastward toward the coast in the northern portions of their range.

Such a strategy would be consistent with Gibo's (1986) hypothesis that there are two major, potentially conflicting, selective pressures on monarchs migrating south in southern Ontario. First, there is selection to minimize effort, and second, there is selection to escape the high latitudes as quickly as possible. Of these two strategies, Gibo maintained that a rapid exiting from the north is often the more important. Migrating with NE tail winds would best allow for a straight-line path to the overwintering sites and would be the optimal response to both selection factors. However, fall weather systems with a westerly wind component are typical of this region. Thus, when monarchs move south under the influence of the prevailing winds, there is a concomitant easterly movement. Gibo found that southward migrating monarchs ignore right crosswinds (N, NW, or W winds), but compensate for left crosswinds (E, SE, and S winds). These behaviors are consistent with an energy efficient and rapid exit from the north, and, if the monarchs avoid flying out over the Atlantic, would lead to the fall build-ups along the east coast. That this is typical monarch behavior is supported both by the historical accounts and our new data.

There is little doubt that monarchs migrating during the fall are affected by dynamic weather systems with their attendant winds. Indeed,

monarchs are, at times, blown off course with disastrous results (summary in Brower 1995). Such phenomena, however, need to be distinguished from the more typical events of this butterfly's travels. While more research needs to be done to furnish a definitive model of the monarchs' southward journey, the elliptical path hypothesis suggested by avian researchers may be a useful framework for understanding the annual fall migration path of monarchs along the Atlantic coast.

The future. A number of factors combine to affect the overall viability of the monarch's eastern migratory population—now considered an endangered biological phenomenon (Brower & Malcolm 1991). On the wintering grounds, abnormally cold winters, deforestation, and local disturbances all play a part (Malcolm & Zalucki 1993). Throughout the monarch's breeding areas and along its migratory routes, the availability of milkweeds, nectaring resources, and roost sites are critical factors. Coordinated, long-term quantitative monitoring projects at breeding areas, along the migratory routes, and at the overwintering sites will provide data that will allow us to document fluctuations in monarch numbers and, perhaps, begin to define factors critical to the conservation of this well-known butterfly's remarkable migration. Let us hope that the long term data do not substantiate the demise of the eastern migration as predicted in Brower and Malcolm (1991).

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