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Stopover Ecology of Monarchs in Coastal Virginia: Using Ornithological Techniques to Study Monarch Migration

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INTRODUCTION

The general migration strategy of monarch butterflies in eastern North America has been well documented and studied (e.g., Brower 1995, 1996; Knight et al. 1999), and their overwintering destination is widely known and has itself been the subject of study (Calvert et al. 1983, 1986; Brower and Calvert 1985). There are also many large-scale, long-term monarch migration monitoring projects, such as Monarch Watch (Taylor 1997), Texas Monarch Watch (Texas Monarch Watch 2002), the Monarch Monitoring Project in Cape May, New Jersey (Walton and Brower 1996), and Journey North (Howard and Davis, this volume). These projects focus on mapping migration routes and documenting seasonal and spatial distribution along the migration pathways. Here, we introduce a new area of research in monarch migration, that of stopover ecology.

Monarchs, like most landbird migrants, must make frequent stops during their migration. Where and for how long birds choose to stop during migration is not random, and it may not be for monarchs as well. Researchers refer to sites at which birds stop as "stopover sites," and to this area of research as "stopover ecology." It is widely accepted that stopover sites represent crucial links between avian breeding and wintering areas, and that suitable sites are necessary for successful migrations (Hutto 1998); birds can rest, avoid predators, forage, and refuel their energy supply (fat stores) at these sites. We suggest that monarchs must face similar needs during migration.

Typically, a researcher studying avian stopover ecology traps birds at areas where they accumulate, individually marks them with numbered leg bands, and makes behavioral observations while the birds are present. Birds rarely stay more than a few days at most sites, so there is usually a constant turnover of individuals. The same should be true for areas where monarchs tend to concentrate each fall.

Determining what constitutes suitable stopover sites for birds involves comparing stopover durations over numerous sites and differing habitats within the migration route (e.g., Davis 2001; Schaub et al. 2001). It is commonly assumed that migrating birds do not stay long in an unsuitable site (Morris 1996); areas where birds routinely stay longer than a day are considered suitable sites. To determine stopover durations, birds must be captured at least twice (e.g., Latta and Brown 1999).

Wing tags for monarchs are easily acquired and used by many butterfly enthusiasts and professional researchers. The main goal of tagging efforts thus far has been to determine migration routes (Taylor 1997), speed of travel (Garland and Davis 2002), and recovery rates in Mexico (Taylor 1997). Here, we used wing tags to determine how long monarchs stop at our site in the same way that ornithologists use leg bands.

Radar counts of birds have been compared to weather variables in many studies (Richardson 1972, 1978, 1990). This research has shown that the most important weather variables influencing the number of landbird migrants in the air are wind direction and speed. In addition, wind conditions influence the numbers and condition of birds that become grounded at stopover sites (Davis 1999). It is clear that monarch flight strategies are influenced by wind conditions (Gibo and Pallett 1979; Schmidt-Koenig 1985). Because of this, wind conditions also affect the counts of migrating monarchs utilizing specific flight strategies (Davis and Garland 2002); monarchs fly close to the ground when they encounter headwinds and soar high during tailwinds. Furthermore, monarchs tagged during favorable wind conditions travel faster than those tagged during unfavorable winds (Garland and Davis 2002). Thus, wind clearly influences the migratory flight of monarchs. However, there is little published information on how wind conditions influence monarchs' stopover decisions.

Our research documents some general aspects of the stopover ecology of monarchs at a known monarch concentration site in coastal Virginia. Specifically, we attempted to determine (1) the number of days monarchs commonly spend at the site; (2) whether there are sex-related differences in stopover durations; (3) the influence of wind conditions on stopover decisions; (4) the influence of wind conditions on stopover duration; and (5) whether the decision to stop is related to the physical condition of the monarchs. We discuss the implications of our results for monarch taggers and explain how they can incorporate our methods into existing programs.

METHODS

Study site

We studied the stopover ecology of monarchs on the southern tip of the Delmarva Peninsula (the outer barrier of the Delaware Bay in Virginia) at the Coastal Virginia Wildlife Observatory (CVWO; in Kiptopeke State Park 5 km from the end of the peninsula), the Eastern Shore of Virginia National Wildlife Refuge (ESVNWR; 1 km from the end of the peninsula), as well as in surrounding areas within a 5-km radius. Further detail of the study site is provided elsewhere (Garland and Davis 2002). We had previously found that large numbers of monarchs migrate through this area each fall and concentrate at the southern tip of the peninsula, allowing large amounts of data collection in a single season.

Field methods

To document the temporal distribution of monarch migration, we used a point-count technique common in studies of migrating raptors. During the fall of 2000 we counted all monarchs seen from the CVWO hawkwatching platform in Kiptopeke State Park. The platform is approximately 5 m above ground, with good visibility in a 360° radius. CVWO employs a hawkwatcher to count migrating raptors from this platform during the fall, and this individual counted any monarchs seen during the raptor count. The daily counting period was divided into three segments—from 1 h after sunrise until 10:00 AM, from 10:30 AM to 1:00 PM, and from 1:30 to 4:00 PM. We considered the total number of monarchs seen from the hawkwatch platform to be indicative of the number of monarchs actively migrating through our study area.

At the end of every day we counted all monarchs at a known accumulation site located near the hawkwatching site. The site is a 1-ha area located at the extreme southern tip of the Delmarva Peninsula that is owned and protected by the ESVNWR. This point of land represents one of the last places where monarchs can stop and rest before crossing the Delaware Bay. We had found previously that monarchs tended to concentrate in this area, roosting in two to three specific trees each fall (Garland and Davis 2002). We visited this site daily just before dusk for approximately 20 min, or on some occasions the next morning just after sunrise, since monarchs do not fly at night (Brower 1995). On each visit, we recorded the number of monarchs seen roosting in the area or flying in the vicinity of the roost trees (or estimated when numbers were larger than 100). Thus, this method targeted monarchs that had stopped migrating at the end of each day.

We also captured and tagged monarchs (using Monarch Watch tags) at specific sites within the CVWO and ESVNWR between 7 September and 28 October. The capture effort varied throughout the study, owing to weather, the number of people capturing or tagging, or other logistic reasons. We recorded the sex of each butterfly and any wing damage. We considered monarchs with damaged wings as those with tears (in either wing) greater than one third the total length of the forewing or holes or pieces missing from either forewing. When we captured a previously tagged individual, we recorded the date and time in order to calculate stopover durations.

The stopover duration of bird migrants is usually calculated by subtracting the date of initial capture from that of the final capture (e.g., Morris et al. 1996; Yong et al. 1998). We modified this by adding 1 day to the result. This addition was necessary since some individuals were recaptured later on the same day they were initially captured, and subtracting the two would have resulted in a stopover of "0 days." Thus, a stopover duration of 2 days indicates that the monarch was present at the site on at least 2 consecutive days. Since we cannot be sure that we captured individuals on the date of their arrival or that the last recapture was on the date of their departure, this method is a conservative estimate of stopover duration (Morris 1996; Morris et al. 1996; Yong et al. 1998). We used a Student *t* test to test for sex-related differences in the average stopover duration of monarchs at our site.

Wind data

We obtained wind data (direction and speed) from a weather station located on the eastern side of the peninsula approximately 100 km north of our site. Wind data were recorded daily at heights ranging from 13 to 1000 m. Wind conditions at this location are similar to those at our site (Garland and Davis 2002). Based on these data, we categorized each day of our study as having overall favorable or unfavorable wind directions and light or strong wind speeds. We assumed that for monarchs heading south-southwest along the Atlantic coast, favorable wind directions included winds from the north, northeast, or north-northeast. All other directions were considered unfavorable. We defined wind speeds under 25 km/h as light and those over 25 km/h as strong.

Data analysis

To determine the relationship between numbers of migrating versus roosting monarchs, we compared the daily numbers of monarchs counted from the hawkwatch platform to the daily numbers of grounded individuals (i.e., counted at the roosting site) with a Pearson correlation test that used the ranks of the actual numbers. We tested for wind effects on the numbers of migrating and roosting monarchs using Kruskal-Wallis (KW) analyses of variance (ANOVAs). The Kruskal-Wallis ANOVA was appropriate for this test (and most of our additional tests) as it is less sensitive to small and variable sample sizes. For this and other tests involving wind conditions, we only used data from days in which 5 or more monarchs were seen during the hawkwatch and roost counts combined.

We tested whether the proportion of monarchs that were recaptured varied with wind conditions. For this test, we calculated the proportion of individuals out of the total number captured each day that we later recaptured. We then tested whether this proportion was affected by the wind conditions in which monarchs were first captured using a Kruskal-Wallis ANOVA on the log-transformed proportions. For this test we pooled light and strong unfavorable directions since there were fewer than 3 days with unfavorable light conditions with captured monarchs. We tested for sex-related differences in the duration of stopover with a Student *t* test.

Finally, we tested for an effect of wind condition on the proportion of monarchs with damaged wings using a Kruskal-Wallis ANOVA. Again we used the log-transformed proportion of individuals with wing damage and pooled strong and light winds in unfavorable directions.

In all tests, significance was accepted when $p < 0.05$. When $p < 0.1$, the result was considered marginally significant.

RESULTS

A total of 1033 monarchs were counted from the hawkwatch platform and 1243 at the roost site during September and October. The bulk of the movement was during October (figure 12.1). Daily numbers of monarchs seen flying from the hawkwatch platform were weakly correlated with the number of roosting monarchs (figure 12.2). In general, on days when large numbers of monarchs migrated, large numbers also roosted at the end of the peninsula. However, on some days large numbers migrated and did not stop, while on other days large numbers of monarchs were counted at the roost but few were seen migrating.

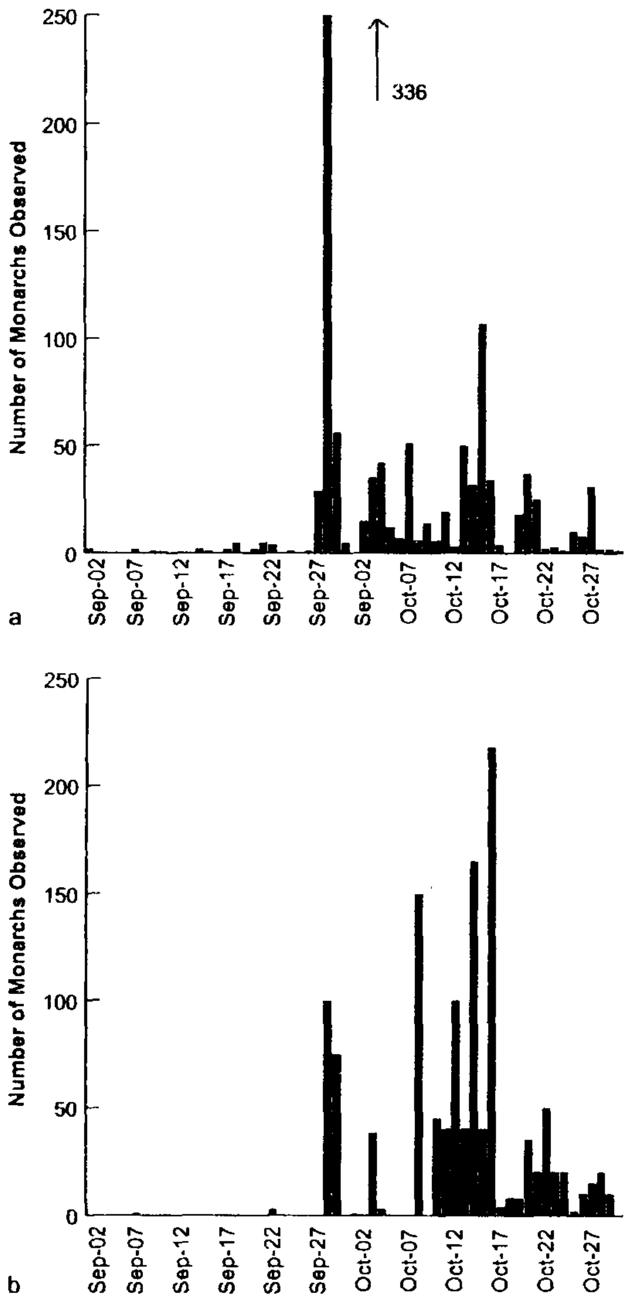

Figure 12.1. Temporal distribution of monarchs in coastal Virginia during the 2000 migration period, as documented by (a) the count from the hawkwatch platform and (b) counts made at the roosting site. The total daily numbers of monarchs seen are presented.

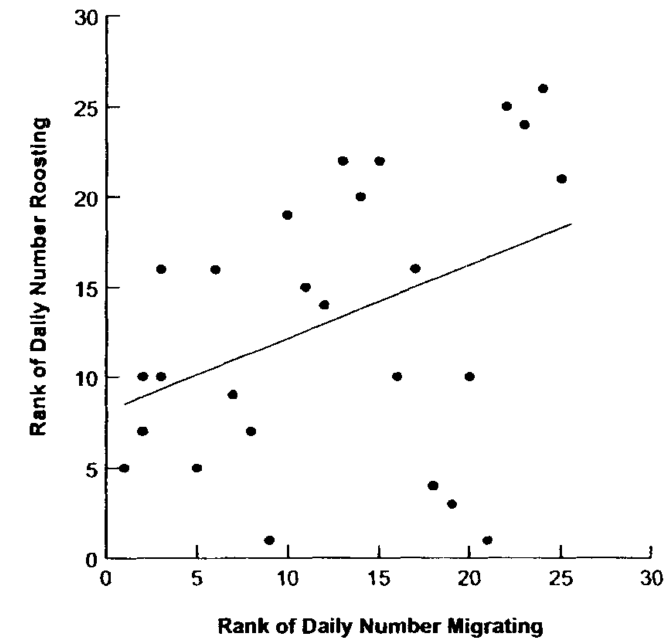

Figure 12.2. Ranks of daily numbers of roosting versus migrating monarchs.

Table 12.1. Tagging summary

Date in 2000	Wind direction	Wind speed (km/h)	Total no. tagged	% Later recaptured
27 Sept	N	26.6	14	0.0
28 Sept	N	15.8	95	1.1
29 Sept	NE	24.1	39	0.0
2 Oct	NNE	39.9	17	0.0
3 Oct	WNW	33.7	11	18.2
7 Oct	N	43.3	41	7.3
10 Oct	W	40.5	37	16.2
11 Oct	NW	35.9	59	1.7
12 Oct	N	20.7	49	4.1
13 Oct	N	25.1	49	4.1
14 Oct	NW	17.3	27	0.0
15 Oct	NW	27.2	24	4.2
16 Oct	NE	6.2	23	0.0
17 Oct	ENE	36.5	16	6.3
19 Oct	NW	34.7	14	7.1
20 Oct	NNE	11.5	37	8.1
21 Oct	SW	25.1	27	0.0
22 Oct	NE	32.8	10	0.0
23 Oct	ENE	29.4	7	14.3
25 Oct	NNE	17.0	9	0.0
26 Oct	SE	13.0	14	7.1
27 Oct	NE	32.2	33	6.1
28 Oct	NW	46.4	13	0.0

Note: Table displays when more than 6 monarchs are tagged, and the associated wind conditions during 2000.

We captured a total of 688 monarchs (46% females) on 36 days from 7 September to 30 October. Most of these captures were in late September and throughout October. We later recaptured 27 (3.9%) of these (table 12.1). Most monarchs stayed 2 days at our site, and few stayed longer than 4 days (figure 12.3). No sex-related differences in the average stopover length were found (t test, $n = 26$, $p = 0.987$).

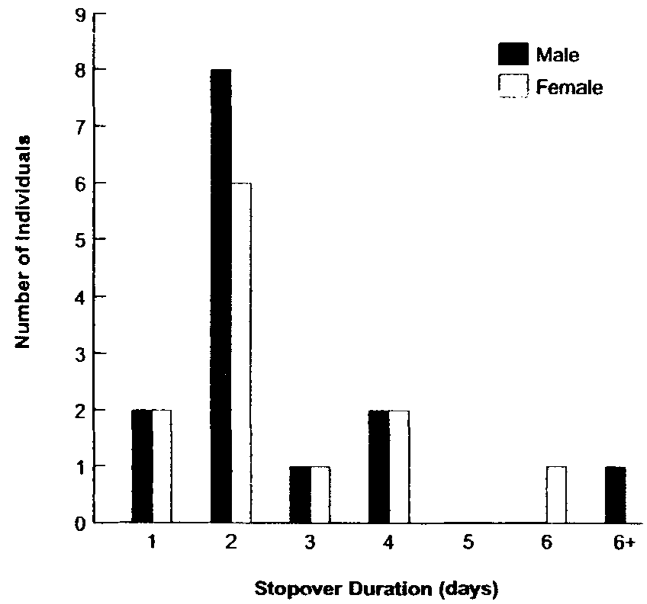

Figure 12.3. Frequency distribution of stopover duration for males and females during 2000. We calculated stopover duration as the date of final capture minus the date of initial capture plus 1.

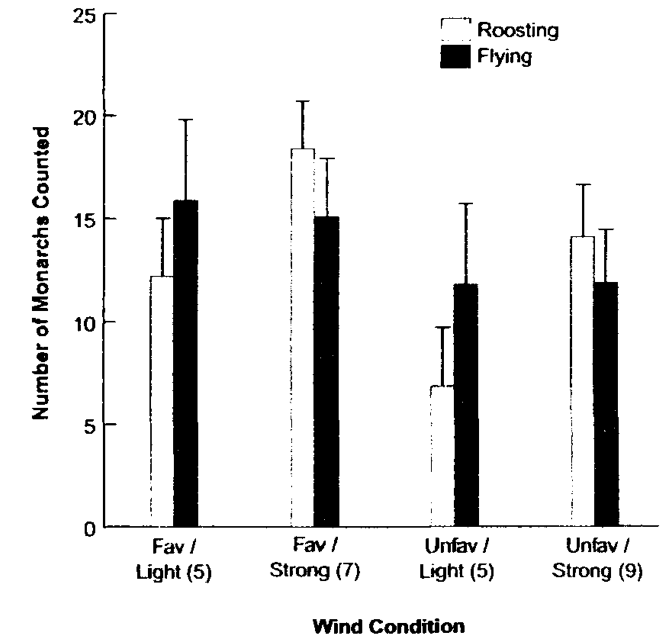

Figure 12.4. Total numbers of migrating monarchs counted from the hawkwatch platform (flying) and grounded monarchs counted at the roost site (roosting) during all wind conditions. The numbers of days in each wind condition category (favorable or unfavorable directions, light or strong wind speeds) are shown in parentheses. Only data from the main migration period (28 September to 28 October) were used. Days when fewer than 5 monarchs were seen (from the hawkwatch and roost counts combined) are excluded.

Effect of wind

The total number of days for which we could record wind conditions was fewer than 30 (we did not include days on which we observed fewer than 5 monarchs). When we categorized the days according to favorable or unfavorable wind directions and light or strong winds, our sample sizes for each treatment were further reduced. Thus the results of our tests involving wind conditions must be interpreted cautiously.

We found a marginally significant effect of wind condition on the numbers of roosting monarchs (KW statistic = 6.79, $df = 3$, $p = 0.079$; figure 12.4), but no effect on the numbers of migrating monarchs (KW statistic = 1.435, $df = 3$, $p = 0.697$). The average proportion of monarchs that were later recaptured was highest when monarchs were tagged during unfavorable wind directions. When wind conditions were favorable (light winds from the north or northeast), the fewest monarchs were later recaptured (figure 12.5), but this result was not statistically significant (KW statistic = 2.55, $df = 2$, $p = 0.279$).

The overall proportion of monarchs with damaged wings was 4.8%. During favorable wind conditions (light winds from the north), the average proportion of monarchs with damaged wings was 4.6% (figure 12.6). During favorable directions and strong winds, the average was 5.2%. During

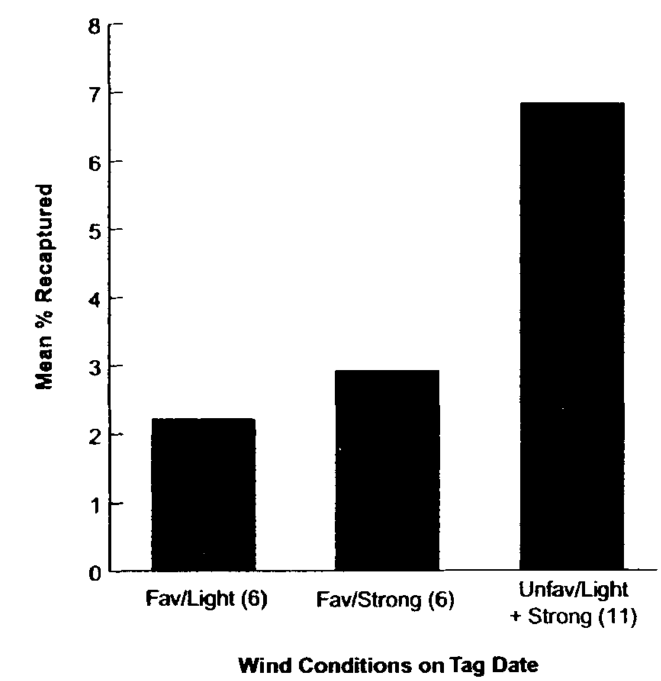

Figure 12.5. Average percentage of monarchs that were recaptured after the initial tagging, during all wind conditions. The numbers of days in each wind condition category (favorable or unfavorable directions, light or strong wind speeds) are shown in parentheses. Days when fewer than 5 monarchs were seen (from the hawkwatch and roost counts combined) are excluded.

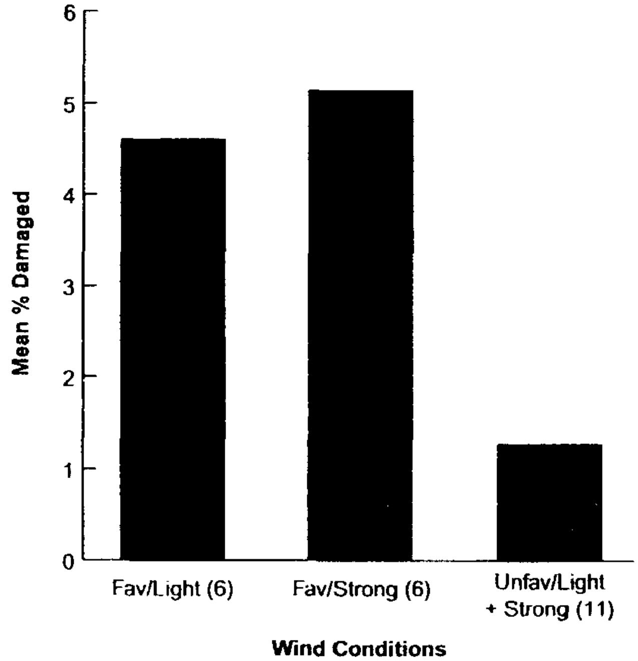

Figure 12.6. Percentage of monarchs with damaged wings captured during each wind condition. The numbers of days in each wind condition category (favorable or unfavorable directions, light or strong wind speeds) are shown in parentheses. Days when fewer than 5 monarchs were captured are excluded.

unfavorable directions and both light and strong winds, only 1.3% of monarchs had damaged wings. These differences were not statistically significant (KW statistic = 1.993, $df = 2$, $p = 0.369$).

DISCUSSION

In this study we adapted techniques used to study bird migration and applied them to the study of stopover ecology in monarchs. This enabled us to provide the first information on this important topic. We monitored the temporal distribution of monarch migration using a point-count method from a hawkwatch platform; temporal distribution has previously only been documented with a driving census (Walton and Brower 1996). We collected information on factors causing monarchs to stop migrating by monitoring a nearby roost site. Finally, by tagging and recapturing monarchs, we could document how long monarchs commonly stop at our site during migration and address factors potentially causing them to stop.

That we only recaptured 27 individuals (3.9%) of the 688 total tagged is not surprising. Ornithologists studying landbird stopover commonly recapture less than 5% of their total captures (e.g., Moore et al. 1990; Morris et al. 1996; Davis 2001). This means, however, that sites where large numbers of monarchs can be captured and multiple years of tagging are necessary to calculate reliable estimates of stopover duration at any given site. The median stopover duration for monarchs at our site in coastal Virginia was 2 days during the 2000 migration season (see figure 12.3), but this result is difficult to interpret since the lack of similar studies in this area of research precludes us from comparing our result to others. Thus it is not known if this duration is a long stopover or a short one. It is generally accepted that long stopovers indicate high-quality sites for landbirds (e.g., Davis 2001), and monarchs may be no different. Nor do we know if this 2-day stopover is indicative of a normal year. More research will provide insight into these questions.

Many of our analyses on the effects of wind conditions on aspects of stopovers did not show significant trends, although there was a marginally significant effect of wind conditions on the numbers of roosting monarchs. However, this could be attributed to the small sample sizes for the tests. Since we could only test for the effect of wind conditions when there were actually monarchs at our site, and since monarchs passed through our site in such a short time, we were left with fewer than 30 days with monarch and wind data for our tests. Researchers who wish to conduct similar studies should monitor for several years in order to collect sufficient data.

One factor that may influence stopover decisions is a monarch's condition. Although the result was not statistically significant, damaged monarchs may have been most numerous during favorable wind directions. When conditions are favorable for active migration, we expect most monarchs to be migrating. Those that we captured on the ground included a considerable number of damaged individuals, indicating that they could not fly or somehow required more time on the ground.

Other factors may cause monarchs to stop migrating or prolong their stopovers. Given the similarities between monarch and bird migrations, we can draw some insight into these possible factors from stopover research on landbirds. It is generally accepted that landbirds stop migrating and set down to forage when their fat supplies are low (Morris 1996). Further, birds stay longer at a stopover site when their fat stores are small than when they are large (e.g., Yong and Moore 1993). Additional research could determine whether monarchs also make stopover decisions based on energy supplies.

It is also generally accepted among ornithologists that landbirds make stopover decisions based on the suitability of the site (Hutto 1998; Latta and Brown 1999; Gellin and Morris 2001). It is not known what constitutes a quality habitat for monarchs' stopover, but nectar sources, roost sites, shelter, or the presence of other monarchs could be important. Further, the presence of many monarchs at a site during migration does not indicate that the site has suitable habitat. Ornithologists have long recognized that the density of individual birds in any habitat is not indicative of its suitability (Van Horne 1983). This is one of the primary reasons why stopover lengths must be compared among several sites to determine the importance of each site during migration.

The stopover ecology of monarchs is a research area that requires more attention by scientists and monarch taggers. Certain annual staging areas have been documented in northern areas, although they have been described as overnight roosting locations rather than stopover sites (Urquhart and Urquhart 1979). However, areas where monarchs roost during migration should also be considered stopover sites, since monarchs interrupt their migration, become grounded for short periods, and subsequently utilize resources (i.e., roost trees, possibly nectar sources) at these sites. These factors are all typical of avian stopovers. The degree to which roosting sites and stopover sites are related is unknown.

It is our hope that these findings will encourage further studies of stopover ecology, an important but little-studied aspect of the monarchs' annual cycle of migration, overwintering, and breeding. The techniques we used in this study were simple and noninvasive and could be easily incorporated into existing monarch or tagging programs. To make meaningful comparisons between geographic locations, results using methods similar to ours from many locations must become available. We need to know where, when, and why monarchs choose to stop during migration. Many scientists and volunteers currently tag monarchs each fall; our results demonstrate that they could easily provide information other than migratory routes to and recovery rates at the overwintering sites. Monitoring the movement and presence of monarchs at specific sites on a daily, standardized basis, and keeping track of associated environmental conditions can increase our knowledge of migration dynamics.

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