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EASTERLY WINDS DISPLACE WOOD-WARBLERS (PARULIDAE) DURING SPRING MIGRATION ALONG THE FLORIDA GULF COAST

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Abstract.—We examine the relationship between wood-warbler migration in spring and wind characteristics at Green Key causeway in Pasco County, Florida. From 2001 through 2010, information on numbers of warblers, wind direction and speed, and frontal passage were collected as migrants returned to the mainland in early morning movements from the end of the Green Key peninsula or from offshore. A total of 42,671 warblers were counted, of which 99% of the warblers identified were Florida/West Indies migrants. A statistical evaluation of the data documented a strong correlation between east and northeast winds and high warbler numbers. Numbers of warblers and strength of easterly winds also were positively related. These results support the conclusion that east and northeast winds tend to drift small, northbound passerines traveling near the coast off the Florida peninsula. As they recover their migration direction, they follow the protruding Green Key peninsula eastward through a narrow defile ("funnel") along the causeway. These data provide a local example of the effect of wind-drift on migrating wood-warblers flying northward over the Florida peninsula in spring.

Under certain conditions, migrant wood-warblers in spring concentrate along the causeway on the Green Key Peninsula, at the entrance to Robert K. Rees Park, Pasco County, on the Gulf coast of the Florida peninsula. One of us (KFT) discovered this phenomenon on 1 May 2001 when warblers were detected flying along a narrow defile on the causeway that joins Green Key Island with the mainland. KFT reported warbler sightings here to the birding community and referred to the location as the "Green Key Funnel". For 10 years he spent most morn-

ings for five to seven weeks each spring on the causeway, counting migrating warblers and recording weather.

Spring warbler migration occurs all along the northern Gulf of Mexico and the Florida peninsula. Warblers migrating in the Gulf region can be grouped into three categories. These are referred to as circum-Gulf migrants, those flying along the Mexican and Texas coasts; trans-Gulf migrants, those flying over the Gulf from Central America and the Yucatan Peninsula; and Florida/West Indies migrants, those following the Florida peninsula (Dunn and Garrett 1997). These routes long have been known to students of bird migration in North America (e.g., Cooke 1915, Lowery 1946). Many studies of trans-Gulf migrants have been conducted on the northern Gulf coast (Moore 1989, Duncan 1994, Gauthreaux 1999, Simons et al. 2004, Gauthreaux and Belser 2005, Gauthreaux et al. 2006). Storm fronts sometimes force trans-Gulf migrants down along the coast and cause significant "fallouts" immediately behind the coast, temporarily preventing migrants from continuing farther north to inland stopover points (Duncan 1994). Elsewhere, as vernal migrants travel northward over land, adverse wind conditions can displace and concentrate migrants on coastlines; this phenomenon of down-wind, lateral displacement from a line of flight is known as "wind-drift" (Mueller and Berger 1967). Green Key provides an apparent example of wind-drift that affects Florida/West Indies migrants in spring as they fly north along the Florida peninsula near the Gulf of Mexico.

Our objective in this study was to understand when and why large concentrations of warblers occur at Green Key. Data on local weather conditions, including wind direction and speed, should permit us to determine the relative roles of wind-drift and fallout events on Green Key during spring migration. Information on the species present in the concentrations should help to determine whether they were characteristic of the Florida/West Indies or trans-Gulf migration routes, as most warblers follow preferred migration routes that emanate most directly from their wintering grounds. We hypothesized that wind-drift acting on migrants near the Gulf of Mexico coast may be an important factor under some wind conditions as they fly northward over the Florida peninsula in spring. We predicted that east and northeast winds would drift many birds westward to the coast, and even over the Gulf. Birds should then redirect their flight to regain their preferred peninsular route early in the morning after sunrise (Baird and Nisbet 1960, Able 1977).

Study Area and Methods

The Green Key peninsula (Fig. 1) is approximately 40 ha in size. It is almost completely mangrove-covered except for several small needle rush (*Juncus roemerianus*) marshes of 2-3 ha each. Along the edge of the peninsula, the tallest and dominant man-

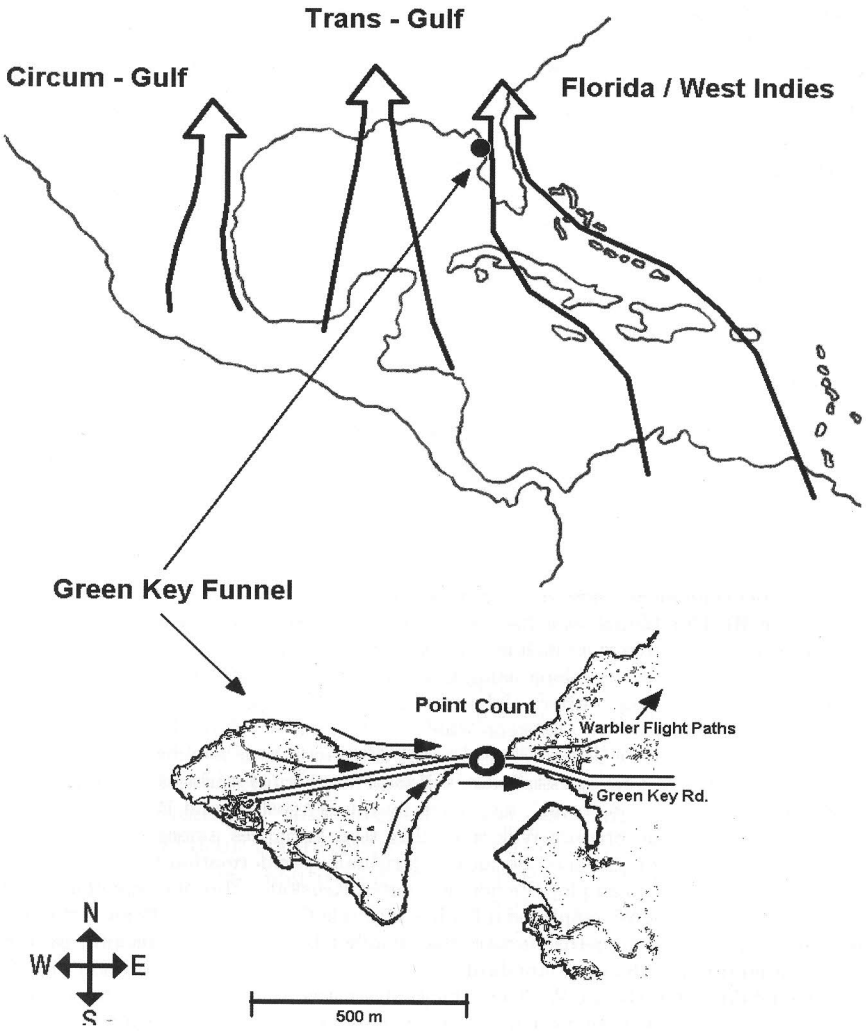

Figure 1. Spring warbler migration routes in the Gulf of Mexico region and the Green Key Funnel location, Pasco County, on the Florida peninsula.

grove species is the black mangrove (*Avicennia germinans*). Smaller white mangrove (*Laguncularia racemosa*) and red mangrove (*Rhizophora mangle*) cover the rest of the land area. Sea myrtle (*Baccharis halimifolia*) and christmasberry (*Lycium carolinianum*) (Wunderlin 2008) also can be found along the road edge and on disturbed ground. At and near the location of the point count along the causeway, Black and White mangroves can be found in a narrow row on both sides of the road, where most of the warblers fly during their eastward, redirected movement.

Green Key protrudes into the Gulf, and its funnel shape guides the warblers exiting the peninsula along the park entrance road. This funnel provided an excellent vantage

point to count migrating warblers each morning. A stationary point count was located at 28.255°N latitude and 82.751°W longitude. The stationary point count method used here included some of the suggested parameters recommended by the University of Florida Extension Service (Hostetler and Main 2008). Coverage was approximately 50 m in all directions because of the unobstructed view, although the suggested point count viewing radius is 20 m.

The counts were started each morning after 06:00 and continued until 09:00 if warblers were still moving through. Count days spanned the period from 7 April to 24 May, 2002 through 2010, but counts during the first count year in 2001 extended from 1-14 May. For the ten years of counting, 268 days of data were collected. All count numbers of warblers were totaled for one-half hour increments. The date, wind direction and speed, and sky conditions also were recorded.

Wind directions used in our analyses were north (N), northeast (NE), east (E), southeast (SE), south (S), and westerly (all winds out of the west). Sample sizes were small for westerly wind directions (SW, W, NW); because warbler numbers were similar in each of these categories, we pooled these data for analysis (W*). Calm conditions with no apparent wind were treated as a seventh, control, category ("None"). Wind speeds were determined from nightly weather reports before count mornings and modified by KFT if they had changed direction or speed at the start of the morning point count. Also noted were any passing storm fronts from the night before. The number of other passerines besides warblers, believed to be migrants and not local nesting birds, were recorded as well. Prairie Warblers that entered the point count coverage area from the east were not counted, as they were regarded as likely to be the local nesting race, Florida Prairie Warbler, (*Dendroica discolor paludicola*). Only Prairie Warblers flying by from a westerly direction were included in the surveys.

Statistical analyses were done using GraphPad Prism 5 software (GraphPad Software, La Jolla, California) with an alpha criterion of 0.05. Mean ± SE are reported here. We looked at the relationship between wind direction and total numbers of wood warblers passing through the Green Key Funnel at dawn until numbers diminished during early morning. The frequency distributions of total numbers of warblers under different wind conditions were non-normal, as judged by the D'Agostino and Pearson omnibus normality test and the Shapiro-Wilk normality test. Variances among wind-direction groups also were heterogeneous. Because logarithmic transformation failed to correct these issues, we chose to employ the nonparametric Kruskal-Wallis one-way analysis of variance on all groups. We employed a Dunn's Multiple Comparison post-hoc test to examine which pairwise comparisons were responsible for an overall significant result. A single outlier (greater than five standard deviations from the mean) was present in each of two wind directions (N and W). The wind analysis was run separately on the dataset with and without these outliers. The results of these analyses were the same, so we report data here without the outliers, which we comment on later. We also performed a linear regression to examine a predicted relationship between observed wind speed and total warblers.

RESULTS

Warbler flights through the funnel only occurred in the early morning just before and after sunrise. Eighty six percent of the total warblers recorded were counted from 06:30 to 08:00. They quickly flew east along the causeway and off the key, not stopping to feed. Some warblers moved through or just over the mangroves as they passed through the causeway funnel, and our assumption was that these birds had

stopped on the Key during the night. An equal numbers of warblers were counted flying high over the Key and causeway and these birds appeared to be flying in off the Gulf. Because of their rapid movement past the count-point, many of the migrant warblers could not be identified. But 30% were identified as they flew close to the observer or stopped momentarily in the mangroves. Out of the 42,671 warblers counted over the ten-year period, 12,885 were identified and included 28 warbler species (Table 1). More than 100 warblers per day were recorded on 86 of the 268 count days (Table 2).

Among the identified warblers, Blackpoll Warbler (*Dendroica striata*) was the most numerous species (26.9%; Table 1). Only 1% of the warblers identified at the point count could be classified as typically trans-Gulf or circum-Gulf migrants, 30% were warbler species that equally use the Florida/West Indies and the trans-Gulf route, and 69% were primarily Florida/West Indies migrants (Table 1, Fig.1).

Total numbers of wood-warblers passing through the Green Key Funnel each morning during spring migration under different wind conditions are shown in Table 2 and Fig. 2. Differences among wind-direction groups were highly significant (Kruskal-Wallis test, $n = 7$ groups, $P < 0.0001$). An *a posteriori* series of pairwise tests showed that only warbler numbers under conditions of E and NE winds were significantly higher than all the others (Table 2). Given the result that E and NE winds were strongly related to the number of warblers observed, we expected a positive correlation between numbers of warblers moving through the Green Key Funnel and wind speed under these conditions. We examined this prediction by determining the product-moment correlation coefficient (one-tailed) between the two variables. Our expectation was confirmed ($df = 111$, $P < 0.01$), and was described by the linear regression: $y = 66.968x - 132.6$, $R^2 = 0.2466$. Thus, wind speed accounted for about 25% of the variation in total warbler movement.

DISCUSSION

The Green Key warbler concentrations do not result from traditional fallout events, as happens during spring migration at nearby Fort De Soto County Park, Pinellas Co., or at other locations along the northern Gulf coast (e.g., Moore et al. 1990, Duncan 1994). Warbler "fallouts" as witnessed by the authors at Fort De Soto Park and elsewhere involve birds grounded by inclement weather conditions associated with frontal systems. These fallout birds spend time actively feeding and resting. Some may linger most of the day at their fallout site or even longer (Simons et al. 2004). At Green Key, the warblers counted moved rapidly to the east, rarely stopping to feed, and appar-

Table 1. Warbler counts for Green Key Funnel 2001-2010. Surveys conducted from 7 April through 23 May[a].

Identified warbler species	Mig.[b]	2010	2009	2008	2007	2006	2005	2004	2003	2002	2001	Total
Blackpoll Warbler (*Dendroica striata*)	F	355	68	508	940	652	37	42	26	19	814	3461
Palm Warbler (*Dendroica palmarum*)	F	600	182	211	430	286	125	458	407	283	7	3053
American Redstart (*Setophaga ruticilla*)	F&T	352	54	94	384	63	28	28	61	98	821	1983
Prairie Warbler (*Dendroica discolor*)	F	169	33	112	119	33	58	100	120	162	58	964
Common Yellowthroat (*Geothlypis trichas*)	F&T	30	85	32	154	8	6	12	28	47	378	780
Black-throated Blue Warbler (*Dendroica caerulescens*)	F	61	38	77	198	89	13	13	14	21	218	742
Cape May Warbler (*Dendroica tigrina*)	F	12	90	103	138	160	8	54	20	7	62	654
Black-and-white Warbler (*Mniotilta varia*) F&T	32	21	23	51	12	6	17	16	12	149	339	32
Northern Parula (*Parula pitiayumi*)	F&T	26	29	17	66	16	11	17	12	23	119	336
Northern Waterthrush (*Parkesia noveboracensis*)	F&T	38	23	34	37	13	8	11	6	0	32	202
Ovenbird (*Seiurus aurocapillus*)	F&T	9	32	5	37	18	1	1	6	7	55	171
Hooded Warbler (*Wilsonia citrina*)	T	0	1	0	40	1	2	3	1	0	0	48
Louisiana Waterthrush (*Parkesia motacilla*)	F&T	0	0	4	17	1	4	1	0	9	0	36
Prothonotary Warbler (*Protonotaria citrea*)	T	2	0	0	25	0	2	1	0	0	1	31
Magnolia Warbler (*Dendroica magnolia*)	T	0	0	0	8	2	0	0	0	0	11	21
Black-throated Green Warbler (*Dendroica virens*)	T	0	1	3	0	3	0	0	0	0	9	16
Worm-eating Warbler (*Helmitheros vermivora*)	F&T	0	1	0	4	0	2	0	1	0	1	9
Tennessee Warbler (*Oreothlypis peregrina*)	T	0	1	0	4	0	0	0	2	0	0	7
Yellow Warbler (*Dendroica petechia*)	C	0	0	0	0	3	1	0	0	0	2	6

[b]Primary spring migration route followed (F) Florida/West Indies, (T) Trans-Gulf, (C) Circum-Gulf, (Dunn and Garrett, 1997).
[a]In 2001 the first count day was 1st May when the funnel activity was discovered. Some years the count was ended by 10 May when no warblers were evident.

Table 1. (Continued) Warbler counts for Green Key Funnel 2001-2010. Surveys conducted from 7 April through 23 May[a].

Identified warbler species	Mig.[b]	2010	2009	2008	2007	2006	2005	2004	2003	2002	2001	Total
Yellow-throated Warbler (*Dendroica dominica*)	F&C	2	1	1	2	0	0	0	0	0	0	6
Yellow-rumped Warbler (*Dendroica coronata*)	F	0	0	0	0	0	1	1	3	0	0	5
Connecticut Warbler (*Oporornis formosus*)	F	0	0	0	4	0	0	0	0	0	0	4
Blackburnian Warbler (*Dendroica fusca*)	T	0	0	0	0	1	0	0	0	0	2	3
Pine Warbler (*Dendroica pinus*)	F	1	0	0	2	0	0	0	0	0	0	3
Chestnut-sided warbler (*Dendroica pensylvanica*)	T	0	0	0	0	1	0	0	1	0	0	2
Cerulean Warbler (*Dendroica ceruleus*)	T	0	0	0	0	0	0	1	0	0	0	1
Black-throated Gray Warbler (*Dendroica nigrescens*)	C	1	0	0	0	0	0	0	0	0	0	1
Bay-breasted Warbler Warbler (*Dendroica castanea*)	T	0	0	0	0	0	0	0	0	0	1	1
Total identified warblers		1690	660	1224	2660	1362	313	760	724	688	2804	12885
Total identified warbler species		15	16	15	20	18	17	16	15	11	18	28
Total warblers counted		5089	1904	3849	7990	4784	1208	4211	2455	2118	9063	42671

[b]Primary spring migration route followed (F) Florida/West Indies, (T) Trans-Gulf, (C) Circum-Gulf, (Dunn and Garrett, 1997).
[a]In 2001 the first count day was 1st May when the funnel activity was discovered. Some years the count was ended by 10 May when no warblers were evident.

Table 2. Warbler counts for the Green Key Funnel with wind data for count days with more than 100 warblers.

Date	Wind speed[a]	Wind direction	Total warblers	Date	Wind speed[a]	Wind direction	Total warblers
15 May 2007	M	E	1751	24 April 2003	M	E	289
23 April 2007	M	E	1714	24 April 2004	M	E	286
4 May 2001	S	E	1567	7 April 2002	L	E	271
5 May 2001	S	NE	1521	28 April 2009	L	E	253
30 April 2006	M	E	1310	21 April 2003	L	E	224
7 May 2001	M	NE	1267	5 May 2004	M	E	220
25 April 2008	L	E	1197	19 April 2005	L	E	205
11 May 2010	M	E	1122	11 April 2004	None	—	203
20 April 2010	L	E	1118	30 April 2009	L	E	187
29 April 2006	M	NE	1079	12 April2010	L	NE	180
9 May 2001	M	NE	1002	18 April 2009	L	E	179
22 April 2007	M	E	974	27 April 2009	L	E	178
3 May 2001	S	E	903	16 May 2007	L	E	172
1 May 2008	L	E	857	19 April 2003	L	E	169
6 May 2001	S	NE	850	8 April 2004	M	S	164
10 May 2010	M	E	799	28 April 2003	M	E	160
2 May 2006	L	NE	790	8 April 2002	L	SE	160
14 May 2007	M	NE	656	26 April 2009	L	E	153
20 April 2003	S	E	652	7 May 2005	L	NE	145
1 May 2006	L	E	638	29 April 2009	L	E	139
15 April 2010	M	NE	569	7 May 2008	L	E	137
8 May 2001	M	NE	535	30 April 2004	L	E	136
10 May 2001	L	E	528	8 April 2006	M	S	136
17 April 2004		E	508	16 April 2010	L	E	135
10 April 2007	M	E	473	10 April 2008	L	E	134
11 May 2001	L	E	439	10 April 2010	L	NE	133
12 April 2006	L	E	431	17 April 2003	None	—	130
10 April 2004	L	W	428	14 April 2009	L	E	129
14 April 2010	L	E	394	14 April 2007	L	E	127
18 April 2004	L	E	380	12 April 2004	S	S	123
21 April 2007	M	NE	373	16 April 2003	None	—	119
23 April 2008	L	NE	372	10 April 2006	M	NE	116
16 April 2004	L	E	370	12 April 2002	None	—	115
19 April 2004	L	E	362	16 April 2002	L	SE	115
7 April 2004	L	E	360	9 April 2008	M	E	112
11 April 2005	L	E	345	19 April 2010	L	E	112
22 May 2007	L	E	338	16 April 2005	M	NE	112
9 April 2004	L	N	329	15 April 2003	None	—	112
24 April 2002	L	E	328	20 April 2004	None	—	110
17 April 2009	M	NE	318	12 April 2005	L	SE	106
24 April 2007	L	E	307	18 April 2003	L	E	103
30 April 2008	L	NE	301	14 May 2008	L	E	101
12 May 2001	L	E	290	4 April 2008	M	NE	101

[a]Wind speeds; None = 0 mph, L = 5 mph, M =10 mph, S = 15 mph.

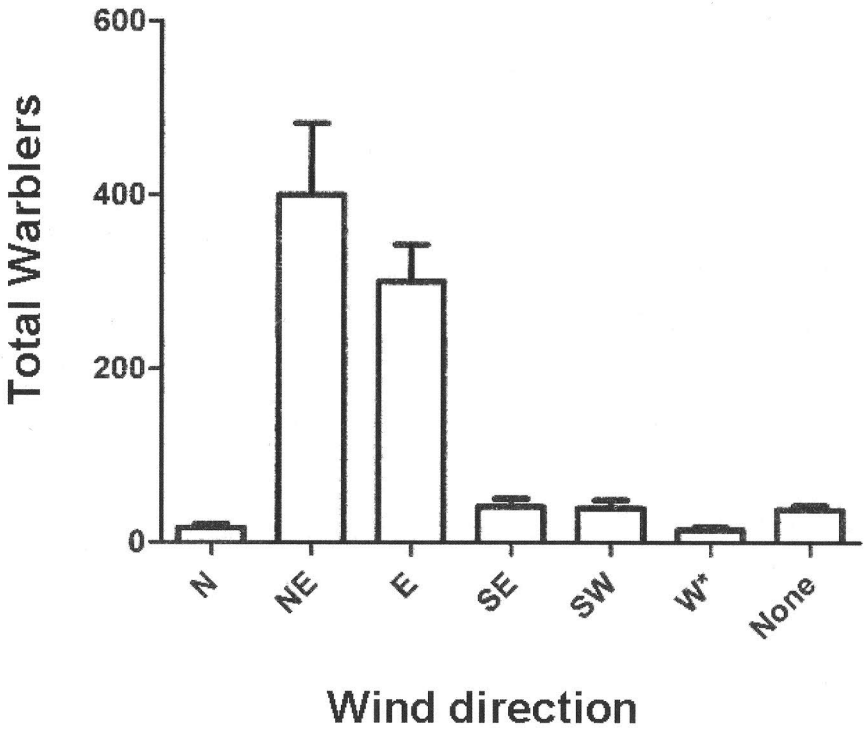

Figure 2. Relationship between wind direction and total warbler movement in the Green Key Funnel. The greatest numbers occurred under easterly and northeasterly wind conditions. W* refers to all westerly winds (SW, W, NW) pooled (see Methods).

ently recovering from wind-drift. We found little evidence that these warblers spent time on the end of Green Key in the vegetation. Even on mornings with high counts, all warblers were gone by a few hours after sunrise.

Nocturnal migration provides an advantage to birds because of atmospheric stability and access to night celestial cues (Raynor 1956), but small migrants such as wood-warblers also are subject to the effects of drift when winds blow across their paths. Night movement would seem to prevent migrating birds from easily using geographic clues to correct for wind-drift as they are pushed towards or over a nearby coastline by crosswinds. Although coastal lights at night would define the Gulf coast to us as a linear line, the reaction of birds to such cues cannot be easily evaluated. During their re-directed, corrective movements following sunrise (Moore 1989), when migrants can detect the effects of drift relative to a coastline more easily, some birds over

the coast land on the key while others offshore fly in from the Gulf. We do not know what fraction of the birds overflying the coast during the night detect and mitigate their situation before dawn and settle on Green Key. Such behavior may depend on moon and sky conditions, and local height of migration. We do show that westward drift occurs at Green Key, and that birds on the key, and those orienting to the key from offshore, follow the peninsula landward at dawn through the narrowed "funnel" as they seek to return to their preferred northward tracks over the peninsula away from the immediate coast.

Our analyses on wind-direction and speed support our prediction of flight displacement of northbound birds based on the wind-drift hypothesis. About 99% of the warblers identified in the concentrations at Green Key consist of species that typically follow the Florida/West Indies route around the east side of the Gulf of Mexico during spring migration. This too supports the conclusion that wind-drifted Florida peninsular migrants are involved at Green Key, as opposed to trans-Gulf migrants.

Blackpoll Warblers use different routes relative to the Florida peninsula in fall and spring. These warblers fly offshore over the Atlantic Ocean directly to South America from the northeastern Atlantic coast in the fall (Hunt and Eliason 1999). As a result, except for occasional storm-driven fallouts along the east peninsular coast, the species is rare in Florida in the fall. In spring, the species migrates northward over the peninsula and off the Florida east coast, so it is more numerous and widespread in Florida on the peninsula at this season (Robertson and Woolfenden 1992, Stevenson and Anderson 1994). Our data (940 counted at the funnel in 2007, 814 in 2001) indicate that vernal wind drift can produce high counts on the central Gulf coast of the Florida peninsula at least as high as those reported on the central east coast (tower mortality in Brevard County: 652 and 611 in 1980 and 1986, respectively [Stevenson and Anderson 1994]). Typically, many Blackpoll Warblers migrate east of the Florida panhandle in spring (Stevenson and Anderson 1994), but they become more numerous even in the western sections of the panhandle "when easterly winds prevail" (Duncan and Duncan 2000). This observation implies that some Florida/West Indies migrants may be drifted far enough offshore over the eastern Gulf of Mexico under the influence of strong east winds that they continue northward to make landfall on the Gulf coast of the Florida panhandle.

In general, west winds did not produce the expected flow of trans-Gulf migrant warblers. Those days with west winds averaged only 42 warblers per day and the majority of these warblers were Florida/West Indies species. Only on a few occasions, when strong west winds associated with a cold front came onto Green Key, did a small number of