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Stormy Seas for Some North American Songbirds: Are Declines Related to Severe Storms During Migration?

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"Many large flocks of birds flew over, coming from the north and flying to the SW. They were more varied in kind than any we had seen before and they were land birds . . . . I know that most of the islands discovered by the Portuguese have been found because of birds."—Christopher Columbus, east of Bermuda, 7 October 1492

Several hypotheses have been presented to explain population declines in long-distance migrant songbirds in eastern and central North America (Rappole 1995). Although declines probably result from the interplay of several factors (Blake et al. 1992), habitat destruction on the wintering grounds in the Neotropics and on the breeding grounds in North America is believed to be a major cause of the declines (e.g. Terborgh 1989, Askins et al.1990, Rappole 1995, Sauer et al. 1996). However, the evidence for a causal link between large-scale population declines and habitat destruction is not strong (Petit et al. 1992).

Many species of songbirds that breed in eastern North America migrate over the western Atlantic Ocean or the Gulf of Mexico to winter in the Caribbean, Central America, or South America (Williams et al. 1977, Williams 1985, Moore et al. 1995, Nisbet et al. 1995). During these transoceanic flights, migrants tend to avoid periods of unfavorable weather, and large-scale movements often coincide with favorable wind conditions (Richardson 1976, Williams et al. 1977, Stoddard et al. 1983, Alerstam 1990). In contrast, songbirds that breed in western North America migrate over land through Mexico and Central America (Moore et al. 1995), where they can make landfall if wind conditions deteriorate. Many birds succumb during unfavorable weather while attempting to cross the Atlantic Ocean (Williams et al. 1977, Alerstam 1990:337–338) and the Gulf of Mexico (Lowery 1946). Consequently, the abundance of songbirds from eastern North America might be affected more strongly by the frequency of unfavorable weather events during migration than would the abundance of songbirds from western North America, because the latter group does not have to migrate over the ocean.

The "storm hypothesis" posits that the abundances of Neotropical species in eastern North America are negatively related to the severity of storms during autumn passage over the ocean. Predictions from the storm hypothesis are that: (1) species that make long flights over the ocean should exhibit greater declines than species that make short flights over the ocean or migrate over land; (2) declines should be greater in the eastern portion of the range of continent-wide breeding species than in the western portion of the range; and (3) the greatest declines should occur in years when storms are most severe during migration.

Methods.—The source of data for songbird abundance and population trends was the North American Breeding Bird Survey (BBS), which is a standardized census that has been conducted by volunteers throughout North America since 1966 (Sauer et al. 1997). The BBS data were divided into eastern North America ("eastern region") and western North America ("western region") based on the BBS scheme (Robbins et al. 1986). Neotropical songbirds nesting in the eastern region were assumed to migrate across the Atlantic Ocean or the Gulf of Mexico, and species nesting in the western region were assumed to migrate over land.

To assess the effect of migration habits on population change, I examined whether 14 species with continent-wide breeding distributions that exhibited a significant decline in abundance ($P < 0.05$) in the eastern region of the BBS (i.e. "ocean" migrants) also declined in abundance in the western region of the BBS (i.e. "land" migrants). The BBS data were collected from 1980 to 1994, when large declines in numbers reportedly occurred (Terborgh 1989, Askins et al.1990, Rappole 1995, Sauer et al. 1996). Each species was assigned a migration category according to the distance it flew between its breeding and wintering locations. Species whose winter distribution overlapped between two or more of the areas (e.g. South America and Central America) were assigned to the closer area. I also compared the annual abundance of 25 species that underwent a significant decline ($P < 0.05$) in the eastern region from 1966 to 1996 with the frequency of storms during the previous autumn migration. To do this, I plotted the annual abundance (Sauer et al. 1997) in the eastern region from 1967 to 1996 against the number of days with storms off the southeastern United States and in the Gulf of Mexico during the previous year's autumn migration (15 August to 15 October; Williams 1985). Tropical storms and hurricanes have been tracked off the United States since the 1950s (Neumann et al. 1993). Because tropical storms and hurricanes stall the movement of cold fronts that are used by songbirds as they depart eastern North America (Williams et al. 1977, Richardson 1979), I

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TABLE 1. Comparison by principal winter distribution (centered in bold) of species with continent-wide breeding distributions in North America that underwent a significant decline in abundance in the eastern region only versus the eastern and western regions of the North American Breeding Bird Survey from 1980 to 1994.

Eastern region only	Eastern and western regions
Mexico, Caribbean, and/or Central America	
Savannah Sparrow (*Passerculus sandwichensis*)	
Red-winged Blackbird (*Agelaius phoeniceus*)	
Central and South America	
Veery (*Catharus fuscescens*)	
Gray-cheeked Thrush (*Catharus minimus*)	
Swainson's Thrush (*Catharus ustulatus*)	
Mourning Warbler (*Oporornis philadelphia*)	
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	
South America	
Common Nighthawk (*Chordeiles minor*)	Black-billed Cuckoo (*Coccyzus erythropthalmus*)
Eastern Kingbird (*Tyrannus tyrannus*)	Olive-sided Flycatcher (*Contopus cooperi*)
Purple Martin (*Progne subis*)	Barn Swallow (*Hirundo rustica*)
Bank Swallow (*Riparia riparia*)	

used the total duration in days of tropical storms and hurricanes over the Atlantic Ocean and the Gulf of Mexico from 15 August to 15 October 1966 to 1995 (USDC 1966–1996) as a measure of unsuitable weather for southbound migrants.

Results and Discussion.—Declines in abundance of songbirds were largely confined to species in eastern North America, and the length of the ocean passage appeared to be an important component of this change. Of the 14 species with continent-wide breeding distributions that underwent significant declines in abundance in the eastern region, 11 declined only in the eastern region, and 3 declined in both the eastern and the western regions (Table 1). Seven of the 14 species wintered principally in South America, 5 wintered in Central America and South America, and 2 wintered in the Caribbean and Central America (Table 1). These results suggest that most of the declines in abundance occurred among long-distance migrants from eastern North America. An analysis for the period 1966 to 1996 showed that an additional 11 species in the eastern region also underwent significant declines, for a total of 25 species (Table 2). Of these 25 species, 13 wintered in South America, 7 wintered in Central America and South America, and 5 wintered in the Caribbean and Central America (Table 2). This distribution was significantly different from an expected equal distribution among winter quarters ($\chi^2 = 6.2$, df = 2, $P < 0.05$), which reinforces my contention that declines occurred mostly among long-distance migrants that bred in eastern North America.

On average, 38.5 days with storms occurred during autumn migration from 1966 to 1995 (range 18 to

TABLE 2. Winter distribution of 25 species that underwent a significant decline ($P < 0.05$) in the eastern region of the North American Breeding Bird Survey.

Principal winter quarters	Species
Mexico, Caribbean, and/or Central America	Whip-poor-will (*Caprimulgus vociferus*), Wood Thrush (*Hylocichla mustelina*), Savannah Sparrow (*Passerculus sandwichensis*), Indigo Bunting (*Passerina cyanea*), Red-winged Blackbird (*Agelaius phoeniceus*)
Central and South America	Veery (*Catharus fuscescens*), Swainson's Thrush (*Catharus ustulatus*), Gray-cheeked Thrush (*Catharus minimus*), Prothonotary Warbler (*Protonotaria citrea*), Mourning Warbler (*Oporornis philadelphia*), Rose-breasted Grosbeak (*Pheucticus ludovicianuus*), Orchard Oriole (*Icterus spurius*)
South America	Black-billed Cuckoo (*Coccyzus erythropthalmus*), Common Nighthawk (*Chordeiles minor*), Chimney Swift (*Chaetura pelagica*), Olive-sided Flycatcher (*Contopus cooperi*), Eastern Wood-Pewee (*Contopus virens*), Eastern Kingbird (*Tyrannus tyrannus*), Purple Martin (*Progne subis*), Bank Swallow (*Riparia riparia*), Barn Swallow (*Hirundo rustica*), Bay-breasted Warbler (*Dendroica castanea*), Blackpoll Warbler (*Dendroica striata*), Canada Warbler (*Wilsonia canadensis*), Baltimore Oriole (*Icterus galbula*)

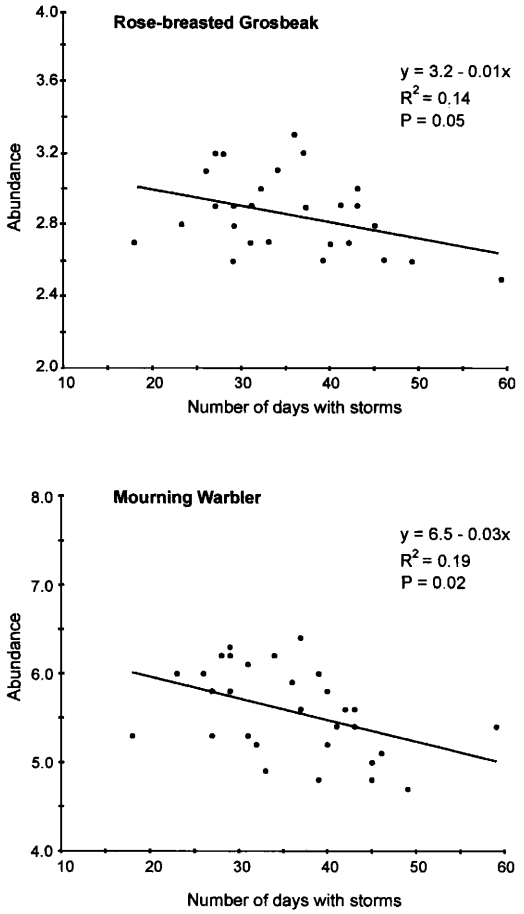

FIG. 1. Relationship between the abundance of Rose-breasted Grosbeaks (top) and Mourning Warblers (bottom) on the Breeding Bird Survey from 1967 to 1996 and the number of days with tropical storms and hurricanes over the Atlantic Ocean and the Gulf of Mexico during the previous autumn migration.

59 days). In the eastern region from 1967 to 1996, the abundance of Mourning Warblers (*Oporornis philadelphia*; $P = 0.016$) and Rose-breasted Grosbeaks (*Pheucticus ludovicianus*; $P = 0.046$) was significantly negatively correlated with the number of days with storms in the Atlantic Ocean and the Gulf of Mexico the previous fall (Fig. 1). The abundance of each of the remaining 23 species was not significantly related to storm frequency ($P > 0.05$). However, it is unlikely that the abundance of most songbirds would closely track the wide swings in storms in the Atlantic and Gulf of Mexico. For example, autumn 1994 was unusually calm, with storms occurring on only 18 days, whereas autumn 1995 was exceptionally stormy, with storms occurring on 59 days (Saunders and Harris 1997). Songbirds might undergo large declines in abundance in response to stormy years that coincide with their fall migration periods, but their inherent rate of increase would require several years to recover to former levels. Consequently, we should expect to find a stronger relationship between population levels on the BBS following stormy years than in calm years. As expected, when the calm year of 1994 was removed from the analysis, the correlations for the Mourning Warbler ($P = 0.004$) and the Rose-breasted Grosbeak ($P = 0.013$) became highly significant. When I removed the calmest years from the analysis (i.e. fewer than 30 days of storms), the abundance of Blackpoll Warblers (*Dendroica striata*; $r = -0.503$, $P = 0.02$) and Rose-breasted Grosbeaks ($r = -0.484$, $P = 0.03$) was significantly negatively correlated with storm frequencies, whereas that of Mourning Warblers was not ($r = -0.35$, $P = 0.10$). It is compelling that a well-known transoceanic migrant, the Blackpoll Warbler (Nisbet et al. 1995), was one of three species whose breeding abundance was negatively correlated with storms over the Atlantic, but it is not clear why the abundances of Mourning Warblers and Rose-breasted Grosbeaks were influenced more by storms than were the abundances of other species.

Many species other than songbirds fly the same transoceanic route between North and South America, and populations of some of these species also have declined. For example, some shorebirds that make transoceanic passages over the eastern Atlantic (Williams 1985) underwent declines in the late 1970s (Morrison et al. 1994) rather than in the 1980s when songbirds traveling the same route declined. However, shorebirds migrate mostly in July and August before the September and October peak of storm activity in the Atlantic, and their declines appear to be related to unusually cold breeding seasons in the arctic (Morrison et al. 1994). Therefore, it is possible that declines in songbirds in North America did not result directly from storm frequency en route, but instead were related to other factors that were correlated with storm frequency during migration. For example, weather during the breeding season and storm frequency during migration might be related to the same climatic factors, both of which could affect songbird numbers (Blake et al. 1992).

Most of the significant declines in my study were confined to songbirds in eastern North America rather than being continent-wide, a finding discovered by other researchers using similar data sets (Askins et al. 1990, Peterjohn et al. 1995). My analysis suggests that for at least three species, estimates of abundance and storm frequency are negatively correlated. Although my results are equivocal for the majority of species, they beg for more data to compare the relative influence of weather on the success of transoceanic migration. For example, information on the seasonal timing of migration is available for many

species, but specific departure dates and annual variation in the ocean-passage component of migration are not available to compare with the timing of storms. The potential number of breeding songbirds in North America is probably determined by the amount of suitable breeding or wintering habitat, but the actual numbers occurring in that habitat each year might be mediated by events such as storm frequency during migration. The number of hurricanes making landfall in the United States in the 20th century varied more widely in the decades preceding the BBS, which suggests that some long-distance migrant birds in eastern North America have undergone wider fluctuations than those detected by the BBS in recent decades.

Winds aloft over the Gulf of Mexico and the Atlantic Ocean are associated with variations in the jet stream, resulting in part from sea-surface temperature in the central and eastern equatorial Pacific (Gray 1984, Saunders and Harris 1997). Moreover, the frequency of storm tracks over the Atlantic and nearby regions are closely related to large-scale climatic events that are believed to originate from sea-surface cooling in the Pacific; when the sea surface cools in the Pacific, winds and precipitation become more variable in North America (Dole 1997). Furthermore, abnormally dry and wet years in North America are thought to be related to the presence of cold water in the equatorial Pacific (Dole 1997). Thus, the effects of storms on migration should be added to the list of possible factors that determine the population levels of eastern songbirds. The fluctuations in abundance of species in the eastern region could represent natural selection against individuals that are poorly prepared to migrate when weather conditions en route became unfavorable. The storm hypothesis yields testable predictions about the quantity of fat reserves required for migration, the timing of departures, and flight speeds of migrating songbirds. Moreover, the hypothesis indicates that the influence of climatic variation on ocean processes (Aebischer 1990) should be extended to include birds that migrate across oceans.

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Measurements of Diving Depth in Dovekies (*Alle alle*)

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Diving seabirds have a three-dimensional foraging habitat, and maximum diving depth is important in defining habitat availability for each species. Therefore, measurements of dive depths and profiles are significant components in many studies of seabird foraging ecology (Burger 1991, Burger et al. 1993, Wilson 1995, Gaston and Jones 1998). The Dovekie (*Alle alle*) is the most abundant seabird that breeds in the high-arctic region of the Atlantic, where it feeds chiefly on small zooplankton (Roby et al. 1981, Bradstreet 1982) that are caught by wing-propelled diving. The actual diving depths reached by foraging Dovekies have not been measured, and apart from indirect evidence, such as dive duration or projections based on dive capabilities of other species, little is known of the diving behavior of Dovekies (Bradstreet and Brown 1985).

Here, we report on field measurements of maximum dive depths attained by adult Dovekies breeding in northwestern Greenland, where most of the world population relies on the rich production of zooplankton in the North Water Polynya between Ellesmere Island and Greenland.

Methods.—The study was performed in a large colony of Dovekies on Hakluyt Island (77°25′N, 72°42′W) in the northern part of the species' range within northwestern Greenland (Boertmann and Mosbech 1998). Adult Dovekies with well-developed incubation patches were captured in mist nets in the colony on 30 July 1997 and between 16 and 21 July 1998 (early nestling period). A total of 56 Dovekies

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