

Tornadic Storm Avoidance Behavior in Breeding Songbirds

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Summary

Migration is a common behavior used by animals of many taxa to occupy different habitats during different periods [1]. Migrant birds are categorized as either facultative (i.e., those that are forced to migrate by some proximal cue, often weather) or obligate (i.e., those that migrate on a regular cycle) [2, 3]. During migration, obligate migrants can curtail or delay flights in response to inclement weather or until favorable winds prevail [4, 5], and they can temporarily reorient or reverse direction when ecological or meteorological obstacles are encountered [6]. However, it is not known whether obligate migrants undertake facultative migrations and make large-scale movements in response to proximal cues outside of their regular migration periods [3]. Here, we present the first documentation of obligate long-distance migrant birds undertaking a facultative migration, wherein breeding golden-winged warblers (*Vermivora chrysoptera*) carrying light-level geolocators [7, 8] performed a >1,500 km 5-day circumvention of a severe tornadic storm. The birds evacuated their breeding territories >24 hr before the arrival of the storm and atmospheric variation associated with it. The probable cue, radiating >1,000 km from tornadic storms [9–11], perceived by birds and influencing bird behavior and movements [12–14], is infrasound (i.e., sound below the range of human hearing). With the predicted increase in severity and frequency of similar storms as anthropogenic climate change progresses [15], understanding large-scale behavioral responses of animals to such events will be an important objective of future research.

Results and Discussion

Approximately 50% of the world's birds migrate, with individuals occupying two or more distinct locations to exploit the relative quality of changing environments [1]. Despite human fascination with avian migration over millennia, many basic questions remain unanswered about how birds migrate and what stimulates migratory behavior [1–3, 16]. Migrant birds

are classified as either facultative or obligate migrants [2, 3, 17]. Facultative migration is stimulated or forced by proximal cues, including abrupt changes in weather [18] or food availability [2]. Obligate, or calendar, migration occurs on a regular schedule and is considered genetically hardwired, or innate [2, 16]. Although obligate migrants can delay flights, change course, and even reverse course during migration in response to unfavorable weather [4, 5, 18–20] or ecological obstacles [6], it is not known whether obligate migrants have the behavioral flexibility to respond with large-scale movements when environmental conditions change on their breeding or wintering grounds [3]. In other words, can obligate long-distance migrants undertake facultative migrations?

We opportunistically addressed this question during a study of migration in golden-winged warblers (*Vermivora chrysoptera*). The golden-winged warbler is a small (~9 g) obligate Neotropical migrant songbird that winters in Central America and northern South America and breeds and raises young in the Great Lakes region and the Appalachian Mountains region of North America [21]. During 2013–2014, we used miniature light-level geolocators ([7–8]; see [Experimental Procedures](#)) to track migration routes and identify wintering locations of adult male golden-winged warblers (hereafter referred to as warblers) breeding in the Cumberland Mountains of eastern Tennessee, USA. Upon geolocator data analysis, we observed that five (all for which the period of interest was recorded) warblers evacuated their breeding territories in apparent anticipation of an approaching severe tornadic storm system.

Between April 13, 2014 and April 27, 2014, geolocator-marked warblers arrived on their breeding territories after a 5,000 km obligate spring migration from eastern Colombia (H.M.S., unpublished data). Between April 27, 2014 and April 30, 2014, a powerful weather system moved east through the central and southern United States [22]. The supercell storms spawned 84 confirmed tornadoes and caused 35 confirmed human fatalities and >one billion dollars (USD) in property damage [22]. Having arrived on their breeding territories 1–13 days earlier, the warblers commenced a facultative migration on April 26–27, 2014, preceding the arrival of the storm system by 1–2 days ([Figure 1](#)). Each warbler took a unique route to the coast of the Gulf of Mexico, ~700 km from their breeding grounds. On April 29–30, 2014, most of the tornadic storm system continued east through North Carolina while heavy rain (>30 cm) fell on the Gulf of Mexico coast [22]. During this period, four warblers remained along the coast of the Florida panhandle, and one warbler continued south along the west coast of Florida and on to western Cuba ([Figures 1E–1G](#)). The evacuation routes taken by some of the warblers were reflective of the northern portions of their fall and spring migration routes ([Figure 1](#)), suggesting they may have followed familiar routes during this event. All five warblers returned to our study sites May 1–2, 2014, where they resumed defending their territories and where we captured them May 3–9, 2014 and retrieved the geolocators.

Although consistent with respect to circumventing the storm system, the movements we observed were independent among individuals (i.e., different distances and directions moved each day), indicating that the movement away from territories (hereafter referred to as evacuation) in advance of the

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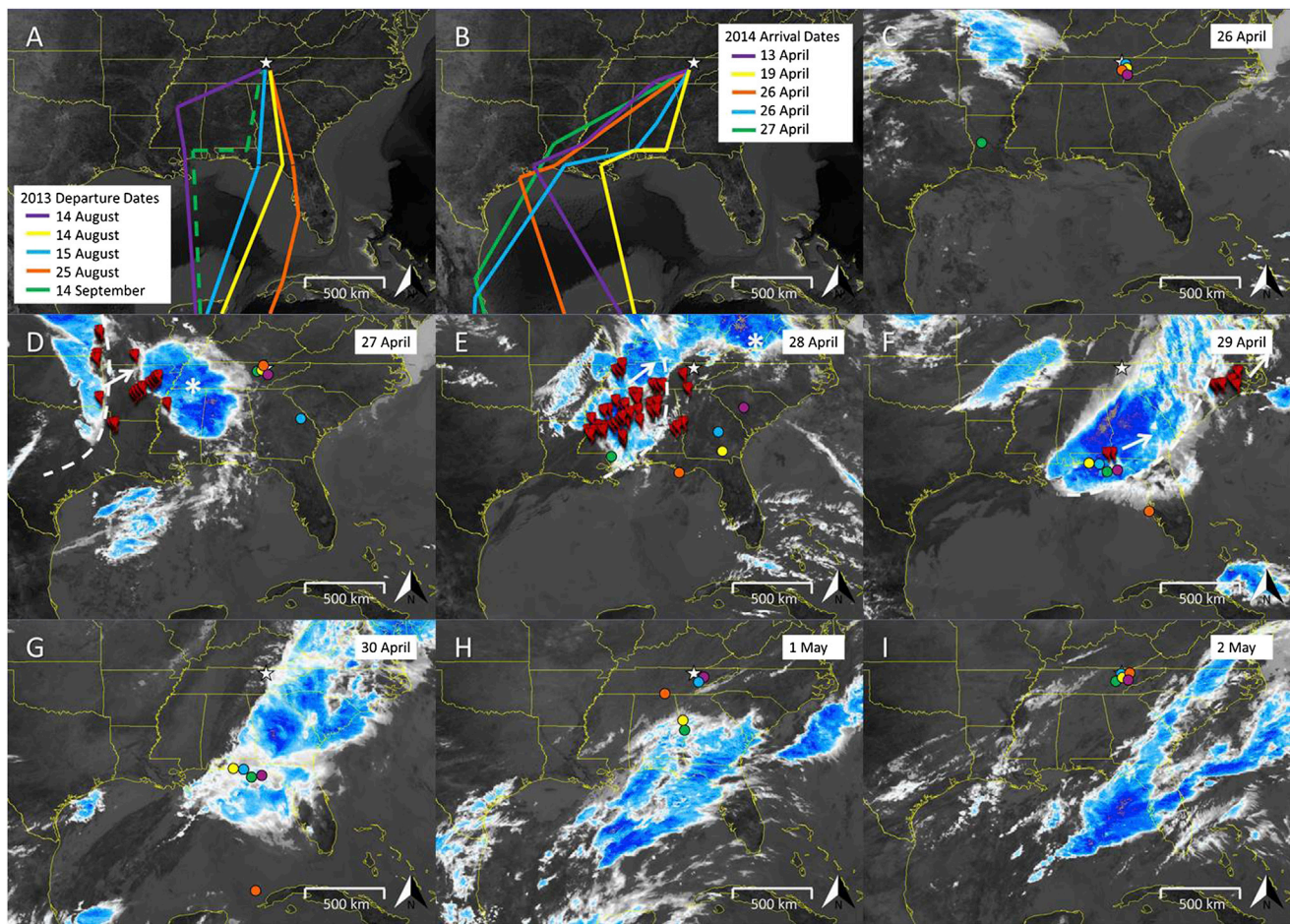


Figure 1. Evacuation Migration Routes Taken by Breeding Golden-Winged Warblers

(A–I) Geolocator-estimated fall 2013 departure dates and migration routes (A) and spring 2014 migration routes and arrival dates (B) of five breeding male golden-winged warblers and their locations (colored circles) between April 26, 2014 and May 2, 2014 (C–I, one day per panel) as a severe tornadic storm developed and crossed the southeastern United States. The one fall migration route traveled within 2 weeks of the equinox is depicted by a dashed line representing reduced confidence in latitude of estimated locations. Our study area (where the birds breed) is depicted by the white star. Weather is depicted as atmospheric water vapor (darker shades of blue indicate colder vapor temperatures modeled from vapor altitude, not necessarily indicating storm intensity); white dashed line represents front edge of the tornadic storm system; red tornado shapes depict tornado locations; and white arrow depicts mean direction of tornado tracks. Daily weather images are from 1200 hr EST, and tornadoes are those that touched down that day (therefore some late-day tornadoes appear ahead of the storm in these images). The asterisk in panels (D) and (E) identifies a low-intensity system that passed north of the study area April 27–28, 2014. Weather data collected by the GOES 13 satellite were retrieved from NOAA’s CLASS, and maps were created with the National Climatic Data Center’s Weather and Climate Toolkit.

approaching storm system was individually based. Transitions (i.e., sunrises and sunsets) in the geolocator data were smooth during this period, suggesting no extraordinary geolocator error due to habitat or weather shading (see [Experimental Procedures](#)). The distances traveled were substantially greater than geolocator error typically caused by anomalous weather events or habitat shading in other studies [23] and in ours. The greatest shading error one week before or after this event produced an estimated breeding location 290 km from our study area, whereas locations during this event were 360–1,460 km from our study area. Further, our study area was not extraordinarily cloudy throughout most of the evacuation period ([Figure 1](#); [Figure S1](#) available online). Therefore, we are confident that the estimated locations represented long-distance movements and were as accurate as estimates of known territory locations.

We did not conduct surveys (see [Experimental Procedures](#)) on any of the study sites on April 29, 2014 because we

performed our own evacuation migration and waited out the storm in Caryville, Tennessee, USA. The five geolocator-marked warblers were not detected during surveys on April 30, 2014, but some (7 out of 23; 30% of expected, based on occupancy of surveyed territories on April 30 in previous years and those observed after the storm) male warblers were observed that day. We observed all five warblers defending territories for the remainder of the nesting season. If evacuation migration is not unique to this species, our observations suggest that migratory fallouts (i.e., large numbers of birds stopping on the United States Gulf of Mexico coast after crossing the Gulf of Mexico during spring migration), which occur when strong weather systems pass north of the coast [24], may include some breeding birds falling back rather than falling out, per se.

Weather-driven facultative migration and even specific timing of obligate migration are purportedly stimulated by one or more environmental cues, including changes in

Facultative Migration in Obligate Migrants

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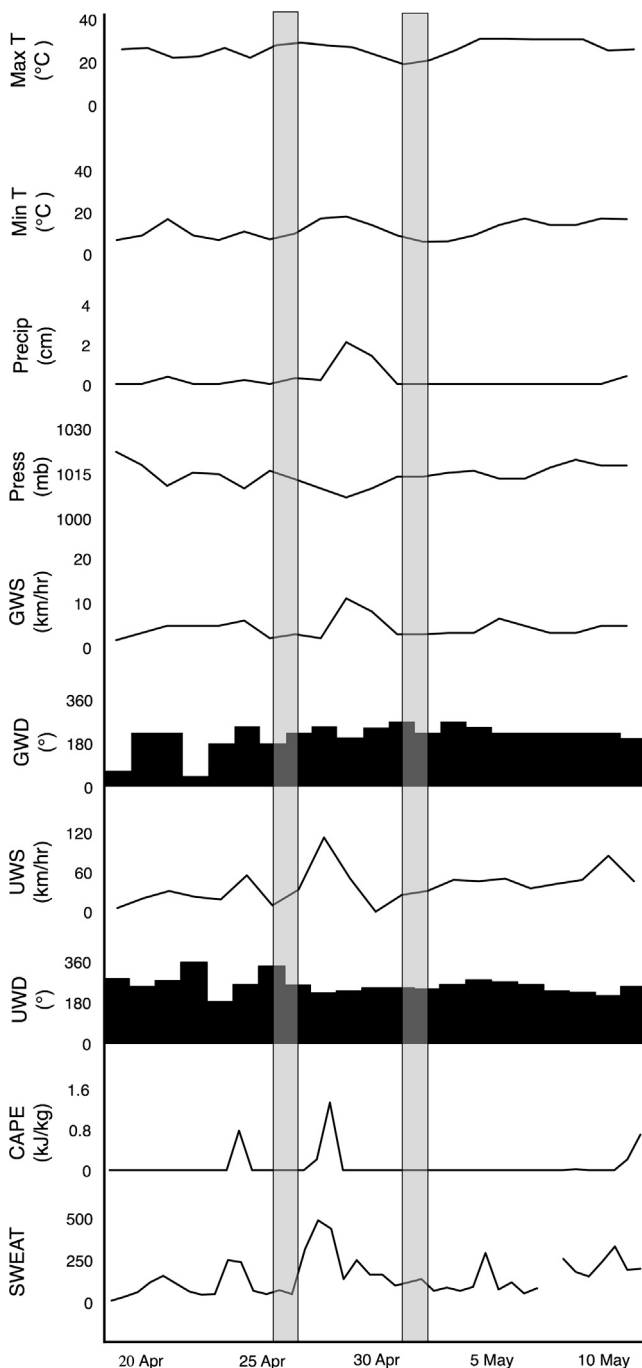


Figure 2. Weather Conditions in Eastern Tennessee, USA during Late April and Early May 2014

Weather variables recorded by the National Weather Service (NWS) and NOAA from April 20, 2014 to May 10, 2014. Maximum and minimum temperature in degrees Celsius (Max T and Min T, respectively), precipitation (Precip), atmospheric pressure (Press), and ground wind speed (GWS) and ground wind direction (GWD; azimuthal wind direction) were measured at the NWS station at Oak Ridge, Tennessee, USA (36.02°N, 84.23°W; elevation: 277 m; 30 km south of our study area). Upper wind speed (UWS) and upper wind direction (UWD) data were collected at a geopotential height of ~1,500 m from atmospheric soundings that occurred at 2200 hr EDT every day near Nashville, Tennessee, USA (36.24°N, 86.56°W; elevation: 161 m; 230 km west of our study area). Convective available potential energy (CAPE; kJ/kg), a measure of the potential energy and instability in the atmosphere, and severe weather threat index (SWEAT; unitless), a relative measure of the likelihood for severe weather to develop, were calculated by

atmospheric pressure, temperature, wind speed and direction on the ground and aloft, cloud cover, and precipitation [17]. We found no evidence that any of these factors could have been used as cues for this evacuation migration behavior (Figure 2; Table S1; Figure S1). The tornadoic storm system arrived at our study area at ~2100 hr on April 28, 2014. The warblers evacuated the study area 1–2 days earlier, when the system was 400–900 km west and moving directly toward the study area (Figure 1) and before atmospheric conditions indicated the potential for severe weather at the National Oceanic and Atmospheric Administration (NOAA) sounding station in Nashville, Tennessee, 230 km west of our study area (Figure 2; Table S1). Furthermore, the environmental conditions experienced by the warblers immediately before they evacuated were not unique among conditions experienced before and after the evacuation event (Figure 2). The evacuation of these warblers independent of any changes in local environmental cues associated with facultative migration suggests a different cue detected by the warblers one or more days before the storm arrived.

Infrasound, or acoustic waves traveling at frequencies <20 Hz, is below the audible range of human hearing, but often travels at amplitudes >100 db [9]. Infrasound from severe tornadoic storm systems can travel thousands of kilometers with little attenuation [9, 10] in the peak frequency range sensed by birds [11]. Responses of multiple bird species to infrasound have been documented [12, 25], the cochlear mechanism of this sensitivity has been identified [13], and the use of natural infrasound for orientation during migration has been described [14]. Birds can detect changes in intensity and Doppler shifts in infrasound [26], suggesting they can sense the movement and direction of severe weather systems from great distances. Although we cannot rule out the possibility that warblers evacuated in response to some other cue, perhaps an undescribed olfactory or visual cue, infrasound is the parsimonious explanation from those available. Perception of infrasound has also been suggested as a possible mechanism for long-distance orientation in nonavian reptiles [27] and communication in dinosaurs [28]. The apparent survival benefit of using infrasound to predict, prepare for, and avoid severe storms or other disasters and the sensitivity to infrasound in nonavian relatives of modern birds leads us to speculate that perception of infrasound may have preceded and possibly facilitated its use as a mapping mechanism during migration [14].

The fitness benefit of obligate migrants sensing the approach of weather systems has been questioned because birds often do not initiate migratory flights until after weather fronts pass and favorable winds prevail [6]. However, this perspective overlooks the immense fitness benefit of surviving by avoiding a severe weather system. In addition to the evacuation migration we observed, it is possible that sensing infrasound from weather systems developing in their flight path contributes to birds reversing or reorienting flights during long-distance obligate migration. Indeed, bar-tailed godwits

NOAA based on additional variables collected during atmospheric soundings at the Nashville sounding station. Severe weather is often associated with increasing CAPE values. SWEAT values >400 signal the chance for the development of severe storms capable of producing tornadoes. SWEAT values <300 suggest little to no risk of severe weather. Shaded bars denote the period during which the birds evacuated the study site (April 26–27) and when they returned (May 1–2). See Table S1 for detailed descriptions of weather variables.

(*Limosa lapponica*) initiate their 14,000 km migration from New Zealand to Alaska, USA only when conditions along the entire route are favorable, and infrasound is a suggested mechanism by which the birds could assess those conditions [19].

That three of the warblers we tracked commenced a >1,500 km round-trip evacuation only 1–2 days after completing their 5,000 km obligate spring migration does not support the hypothesis that long-distance migrant birds travel at or near the limits of their physiological or energetic capabilities [29]. Rather, our observations suggest that at least some long-distance migrants can fly substantially farther than their obligate seasonal movements require if need be. Although much of adult annual mortality in migrant songbirds might occur during spring and fall migration [30], songbirds expend roughly twice as much energy during stopovers as they do during migratory flight [31], suggesting that flying around a storm can be more energetically cost effective than enduring it on the ground.

Anthropogenic climate change is predicted to increase the frequency and severity of storms like the supercell tornado outbreak that passed through our study area in late April 2014 [15]. It is therefore notable that the strongest tornado outbreak ever recorded in North America occurred 3 years and 2 days prior to the event we observed in the same geographic region [20]. If such “storm of the century” events continue to occur every few years, it will be important to describe behaviors that might mitigate direct mortality but could also increase energetic demands on breeding birds. Our observations lead to questions about whether birds would evacuate if a similar storm occurs later in the season when birds are more invested in nests or fledglings or if males, but not females, would evacuate and what the energetic demands and fitness consequences might be for these behaviors. With advancements in miniaturization of geolocators and other tracking devices, the coming years promise to be an exciting time for describing large-scale responses by birds to extreme weather events.

Experimental Procedures

Data Collection

We studied golden-winged warblers breeding on three mountaintop reclaimed strip mines (three study sites in one study area) in the North Cumberland Mountains Wildlife Management Area of northeast Tennessee, USA (36 16 08N, 84 17 38W). We captured, marked, and collected data from warblers following Protocol #561, approved by the University of Tennessee Institutional Animal Care and Use Committee. In May 2013, we captured 20 adult male warblers on their breeding territories using mist nets and playback of recorded songs to simulate territorial invasion [31]. Of the 20 warblers, four were second-year (SY) birds (first breeding season), and 16 were after-second-year (ASY) birds (at least their second breeding season) when marked in 2013. Each bird was marked with a light-level geocator (Biotrack model ML6340) with ($n = 10$) or without ($n = 10$) a 5 mm light stalk. Geolocators were attached to birds using a leg-loop harness identical to the design used by Streby et al. [32] for radio transmitter attachment in this species but made of 0.5 mm black Stretch Magic jewelry cord (Pepperell Braiding Company) instead of degradable elastic. Geolocators were 0.45–0.51 g (~5% of body mass) including harness. Geolocators caused no apparent effects on return rates, with 47% (9 out of 19; one censored after returning without geocator) of geocator-marked warblers and 42% (5 out of 12) of color-banded control warblers returning in 2014. In 2014, we surveyed the study sites from April 21 to May 15 for returning birds. Of the 20 geocator-marked birds, ten returned and were observed on our study sites. Of the ten birds that returned, one had dropped the geocator and harness at some unknown time (censored from comparison with control birds), one was captured and the geocator was removed on April 24, 2014 (before the storm event), two were not captured despite tremendous effort between May 2, 2014 and May 20, 2014, and one was observed on

its territory on multiple days preceding the storm but was not seen after the storm and therefore not captured. The remaining five geocator-marked warblers are those for which movements are reported here. Of those five warblers, four were ASY birds and one was an SY bird when marked in 2013.

Analysis

We used BASTrak software (Biotrack) to download, decompress, and analyze light intensity data from geolocators and to estimate daily noon locations. We followed methods described by Delmore et al. [33] for data analysis. Briefly, we used light intensity to identify timing of local sunrises and sunsets, using a threshold value of 1 from the arbitrary light range of 0 to 64 recorded by the geolocators [33]. We calibrated locations to the study area when birds were known from ground truthing to be on their territories (May 2013–June 2013) and in the days before and after evacuation (April 2014–May 2014). Latitude and longitude of locations were exported and plotted with weather imagery using the National Climatic Data Center's Weather and Climate Toolkit (version 3.7.4; National Climatic Data Center). We downloaded weather data and imagery from NOAA's Comprehensive Large Array-Data Stewardship System (CLASS) server collected by the Geostationary Operational Environmental Satellite (GOES) 13.

Supplemental Information

Supplemental Information includes Supplemental Experimental Procedures, one figure, and one table and can be found with this article online at <http://dx.doi.org/10.1016/j.cub.2014.10.079>.

Author Contributions

H.M.S., D.E.A., and D.A.B. designed the study; H.M.S., G.R.K., S.M.P., J.A.L., and D.A.B. collected field data; H.M.S. and G.R.K. analyzed data; and all authors, led by H.M.S., wrote the manuscript.

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