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Fat, weather, and date affect migratory songbirds' departure decisions, routes, and time it takes to cross the Gulf of Mexico

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Approximately two thirds of migratory songbirds in eastern North America negotiate the Gulf of Mexico (GOM), where inclement weather coupled with no refueling or resting opportunities can be lethal. However, decisions made when navigating such features and their consequences remain largely unknown due to technological limitations of tracking small animals over large areas. We used automated radio telemetry to track three songbird species (Red-eyed Vireo, Swainson's Thrush, Wood Thrush) from coastal Alabama to the northern Yucatan Peninsula (YP) during fall migration. Detecting songbirds after crossing ∼1,000 km of open water allowed us to examine intrinsic (age, wing length, fat) and extrinsic (weather, date) variables shaping departure decisions, arrival at the YP, and crossing times. Large fat reserves and low humidity, indicative of beneficial synoptic weather patterns, favored southward departure across the Gulf. Individuals detected in the YP departed with large fat reserves and later in the fall with profitable winds, and flight durations (mean = 22.4 h) were positively related to wind profit. Age was not related to departure behavior, arrival, or travel time. However, vireos negotiated the GOM differently than thrushes, including different departure decisions, lower probability of detection in the YP, and longer crossing times. Defense of winter territories by thrushes but not vireos and species-specific foraging habits may explain the divergent migratory behaviors. Fat reserves appear extremely important to departure decisions and arrival in the YP. As habitat along the GOM is degraded, birds may be limited in their ability to acquire fat to cross the Gulf.

migration | ecological barrier | Gulf of Mexico | songbirds | weather

During migration, animals encounter ecological barriers, inhospitable environmental features that prevent or impede movement due to increased risk of mortality from starvation, predation, collision, and severe environmental conditions (e.g., weather for aerial migrants, aquatic temperature or chemical gradients for aquatic migrants) (1–5). Because barriers can have important consequences on survival and future reproductive success (6), animals have evolved behavioral, morphological, and/or physiological means to safely negotiate them (7–9). Barriers can include large geographic features (e.g., large water bodies, deserts, mountains), inhospitable land cover types (e.g., agricultural "deserts"), anthropogenic structures (e.g., tall buildings, towers, dams, weirs), and unfavorable weather and aquatic conditions (e.g., droughts, storms, strong temperature gradients), although the extent to which any of these functions as a barrier to migration varies (4, 5, 10–12).

Approximately two thirds of all songbird species and millions of individuals breeding in eastern Canada and the United States encounter the Gulf of Mexico (GOM) while migrating to tropical or subtropical wintering grounds in the Caribbean, Mexico, and Central and South America (13). Unfavorable weather conditions combined with a lack of resting and refueling opportunities over open water can be lethal (14, 15). Accounts of thousands of songbirds washing ashore (16), exhausted songbirds alighting on offshore structures or boats (17), terrestrial birds in the stomachs of sharks (18), and flights away from the coast in seasonally inappropriate directions (19, 20) reinforce the view that crossing the GOM presents considerable risk. However, though the GOM is often considered a barrier (17, 20), large numbers of birds routinely cross it (21–25) and arrive on the opposite coast in good energetic condition (26), suggesting that the Gulf is not inherently a barrier. Rather, the risks of crossing the GOM and the extent to which it functions as a barrier appear to be determined by intrinsic and extrinsic factors—notably, weather (10, 19, 27) and fat reserves (20, 28). By coordinating the timing and orientation of departure with favorable conditions, crossing large bodies of open water can be quick, energy efficient, and safe (2).

Significance

Bird migration has captivated the attention of scientists and lay people for centuries, but many unanswered questions remain about how birds negotiate large geographic features during migration. We tracked songbirds across the Gulf of Mexico to investigate the factors associated with birds' departure decisions, arrival at the Yucatan Peninsula (YP), and crossing times. Our findings suggest that a bird's fat reserves and low humidity, indicative of favorable synoptic weather patterns, shape departure decisions. Fat, date, and wind conditions predict birds' detection in the YP. This study highlights the complex decision-making process involved in crossing the Gulf and its effects on migratory routes and speeds. A better understanding of the factors influencing migration across these features will inform conservation of migratory animals.

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Under such conditions, crossing features like the GOM should be preferred to circumnavigating them, because crossing can substantially reduce travel distances and time while reducing exposure to predators and pathogens (8, 29). However, how departure decisions and conditions affect the fate of songbirds crossing large geographic features is unknown, hindering our understanding of how songbirds negotiate ecological barriers.

The risk of crossing the GOM is dynamic and unpredictable due to spatiotemporal changes in atmospheric conditions over water as well as the variable energetic condition of birds. Small songbirds that incorrectly assess risk incur large fitness consequences; therefore, natural selection presumably has favored flexible migration strategies (4, 24). Under such strategies, animals may use decision rules to assess risk by considering intrinsic and extrinsic factors at the time and location of departure. For birds crossing the GOM, an ∼1,000-km nonstop flight that can take more than 24 h, maintaining a positive energy balance is likely the primary consideration when assessing risk (30). After prolonged and/or energetically inefficient flights, migrants may run out of energy reserves and die. Longer flights also may increase exposure to inclement weather. Therefore, migrants should make decisions that minimize both time and energy expenditure.

Intrinsic factors are expected to influence birds' decisions about whether and when to migrate across the GOM; such factors include fat reserves, age, and wing aerodynamics (e.g., wing length). The role of these factors is likely species specific. Energetic reserves (primarily fat but also protein) contribute to reducing the risks of migrating where foraging options are scarce and/or energetic demands are elevated (31, 32). Age may affect migratory decisions because older individuals might use previous experience to optimize their travel and assess and manage risk (33, 34). Individuals, or species, with longer, more-pointed wings and lower wing loading benefit from more energy efficient flight and are more likely to attempt longer, nonstop flights (35). Furthermore, evidence suggests that species with wing morphology adapted for long-distance flight can fly in a broader range of weather conditions than birds with morphologies less adapted for long-distance flight (9).

Atmospheric conditions are the primary extrinsic factors influencing decisions regarding migratory flights, particularly over water bodies with limited opportunities to land (36). Wind plays a critical role, affecting departure date and migratory directions, routes, speeds, flight durations, and energy consumption (35, 37–40). Decisions to depart stopover sites and initiate flight over large water bodies also are influenced by barometric pressure, temperature, relative humidity, and short-term trends in these variables, which are indicative of synoptic weather patterns and may provide information about future weather conditions (14, 19, 36).

Studies of migratory departure decisions of small birds along edges of large geographic features, including the GOM, have contributed substantially to our understanding of how they assess and manage risk at the onset of flight (20, 28, 31, 41), but the consequences of these decisions on migratory routes, crossing times, and arrival on the other side are unknown. Light-geolocator studies have advanced our understanding of general migration routes of small birds in relation to geographic features and overall rates of migration (42), but the low spatial and temporal precision of these studies do not permit analyses of how behaviors are informed by dynamic intrinsic and extrinsic variables at fine scales. Though GPS loggers and satellite transmitters have become smaller (43), nonarchival units with fine temporal resolution are not nearly small enough for small songbirds. Because of differences in flight mechanics, physiology, behavior, and time of migration (day vs. night), we do not expect songbirds to follow the same behavioral rules to guide their migration as the shorebirds, waterfowl, and raptors that have been tracked with these larger nonarchival technologies (2, 4, 11). Automated radio telemetry, however, allows for the collection of precise spatial and temporal data on animal movements without the need to retrieve the device (20), and transmitters can be deployed on animals as small as 0.3 g (44). Automated telemetry coupled with favorable geography facilitates detection over a large area, providing a tool to link departure decisions, arrival status, and crossing times with intrinsic and extrinsic conditions.

To understand how small Neotropical migratory songbirds negotiate the GOM, we established two networks of automated radio telemetry systems to record departure behavior of three species from coastal Alabama (AL) and detect birds in the northern Yucatan Peninsula (YP) following passage across the Gulf (Fig. 1, *SI Methods*, Fig. S1). For species with winter distributions in southern Mexico and Central and South America, birds departing AL under prevailing winds should arrive at the YP (45), a landmass known for its importance to Neotropical migrants (22). Using this network, we first examined birds' departure decisions (over water, over land, or no departure, i.e.,

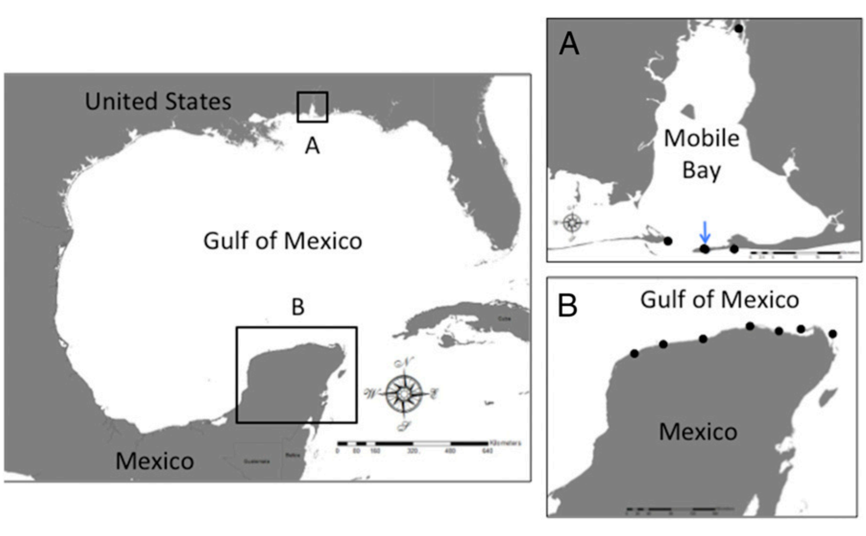

Fig. 1. Locations of automated telemetry towers around the Gulf of Mexico. (*A*) Locations of our capture site (blue arrow) and tracking towers in AL (black circles). (*B*) Locations of tracking towers along the northern Yucatan Peninsula (black circles). The distance between the two regions ranges from 950 to 1,040 km.

stopover) from coastal AL in relation to intrinsic (species, age, fat, wing length) and extrinsic (weather, date) variables to identify the conditions that favor initiation of flights across the GOM. Second, using information on known arrivals at the YP and crossing times from AL to the YP, we identified the conditions suitable for flights across the GOM and examined whether departure decisions from AL accurately predicted arrival at the YP. Third, we evaluated factors influencing crossing times to the YP. By detecting songbirds in the YP, ~1,000 km away from their departure site in coastal AL, we provide unique insight into the factors and conditions that minimize risk of crossing the GOM and influence its role as an ecological barrier.

Results

Departure Decisions. We recorded departure behavior and arrival status of 119 Swainson's Thrushes (SWTH; *Catharus ustulatus*), 25 Wood Thrushes (WOTH; *Hylocichla mustelina*), and 100 Red-eyed Vireos (REVI; *Vireo olivaceus*; *SI Methods*). Eighty-five percent of birds departed coastal AL on the evening of capture; of these, 43% departed southward (over water; bearing >90° and <270°) and 57% departed over land (bearing ≥270° or ≤90°) in directions consistent with reverse movement or circum-Gulf routes. Fifteen percent of radio-tagged birds did not depart the evening of capture and stopped over at the site for more than 24 h.

Departure decisions varied significantly between vireos and the two thrush species [generalized linear mixed model (GLMM): $F_{2,140} = 8.84$, $P = 0.0002$, thrush species combined]. Most vireos departed over land, whereas most thrushes departed over water (Fig. 2, *SI Methods*, Fig. S2). The percentage of birds that stopped over (i.e., did not depart the day of capture) was similar among species, although the stopover duration of vireos was more than twice as long as that of either thrush species (median: REVI = 7.5 d, SWTH = 2.6 d, WOTH = 3.2 d; GLMM: $F_{2,10} = 7.60$, $P = 0.0098$). Regardless of species and departure direction, most individuals departed the capture site within an hour after sunset (*SI Methods*, Fig. S3).

A combination of fat, species, atmospheric humidity, and 24-h change in humidity predicted departure decisions from AL [Fig. 3; correct classification rate (CCR) = 68.9%, κ = 0.474, $P < 0.0001$]. Our classification and regression tree (CART) analysis accurately predicted 76.1% of birds that selected over-water departures. On nights when humidity was low (<62%), a condition that generally occurs following the passage of a cold front (36), vireos and thrushes with high fat reserves (scores of 4–5) departed south over the GOM. When humidity was >62%, thrushes only departed over water when they had maximum fat reserves (score of 5). In contrast, vireos generally did not depart over water when humidity was >62%, regardless of how much fat they carried.

Migrants that departed over land or stopped over in AL were correctly classified 66.9% and 62.5% of the time, respectively. Birds of all species with moderate fat reserves (scores of 2–3) and vireos with high fat reserves (scores 4–5) departing on days with humidity >62% were most likely to depart over land. Lean birds (fat scores 0–1) were likely to depart over land if humidity dropped by at least 5% over the previous 24 h, but stopped over if humidity increased.

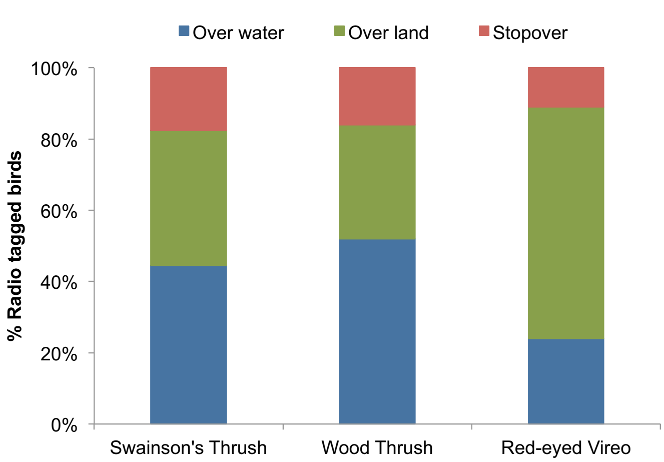

Fig. 2. Percentage of birds selecting each departure decision at our coastal AL study site within 24 h of capture.

Arrival at the YP. The percentage of birds arriving at the YP varied among species; a significantly larger percentage of SWTH and WOTH (31% and 28%, respectively) were detected in the YP than REVI (16%; GLMM: species $F_{2,185} = 27.96$, $P < 0.0001$; Fig. 4). Though there was no overall effect of departure decision on arrival at the YP (GLMM: departure group $F_{2,185} = 1.42$, $P = 0.2431$), there was a significant interaction between species and departure decision (GLMM: species × departure group $F_{3,185} = 99.07$, $P < 0.0001$). Thrushes that departed over water had a greater probability of being detected in the YP than those that did not depart over water ($t = 3.08$, $P = 0.0024$); this was not true for Red-eyed Vireos ($t = 0.19$, $P = 0.8479$).

Considering only the 90 birds that departed over water the evening of capture, 26 traveled directly to the YP (arrived <35 h after departure from AL), 7 traveled indirectly to the YP (arrived >70 h after departure), and the remaining 57 were not detected. No birds detected in the YP had crossing times between 35 and 70 h. Three variables predicted whether birds initiating over-water flights were detected in the YP: departure date, fat, and wind profit (Fig. 5; CCR = 77.6%, κ = 0.462, $P = 0.0068$).

The CART model accurately predicted the arrival of 73.9% of over-water departing birds at the YP following direct, trans-Gulf flights. Birds had a high probability of completing trans-Gulf flights to the YP if they departed after September 24, carried large fat reserves (score of 5), and had a wind profit greater than −2.4 at the time of departure (light headwinds or tailwinds). The model was unable to accurately classify birds that arrived >70 h following departure, likely because conditions at their actual departure location and time were unknown.

The CART correctly classified 76.1% of migrants that departed over water but were not subsequently detected in the YP. Birds that departed before September 24 or departed afterward but with fat scores less than 5 were unlikely to be detected at the YP.

Crossing Time. When considering all birds that arrived at the YP, REVI took significantly longer to travel between the AL capture site and the YP (median = 208.6 h, $n = 16$) than SWTH (26.3 h, $n = 37$) and WOTH (28.4 h, $n = 7$; GLMM: $F_{1,28} = 4.50$, $P = 0.0429$), because more vireos departed over land and flew indirectly to the YP. Eighty-one percent of all REVI flew indirectly to the YP compared with 41% of SWTH and 29% of WOTH (GLMM: $F_{1,30} = 3.77$, $P = 0.0616$; thrush species combined for analysis). Age and wing length were not related to crossing time when we considered all arrivals (GLMM; age: $F_{1,28} = 0.36$, $P = 0.5534$; wing length: $F_{1,28} = 2.06$, $P = 0.1620$).

Birds that made direct flights across the Gulf on the evening of capture (79% of arrivals), for which we had data on intrinsic and extrinsic variables at the time of crossing, had a significant negative relationship between trans-Gulf flight duration and mean wind profit (GLM: $F_{1,21} = 20.96$, $P = 0.0002$; *SI Methods*, Fig. S4). There was no relationship between trans-Gulf flight duration and species ($F_{2,21} = 0.10$, $P = 0.9025$), age ($F_{1,21} = 0.09$, $P = 0.7712$), fat ($F_{1,21} = 0.47$, $P = 0.4986$), or wing length ($F_{1,21} = 0.12$, $P = 0.7378$). Trans-Gulf flight times ranged from 14.9 to 34.6 h (mean ± SE: 22.4 ± 5.1 h).

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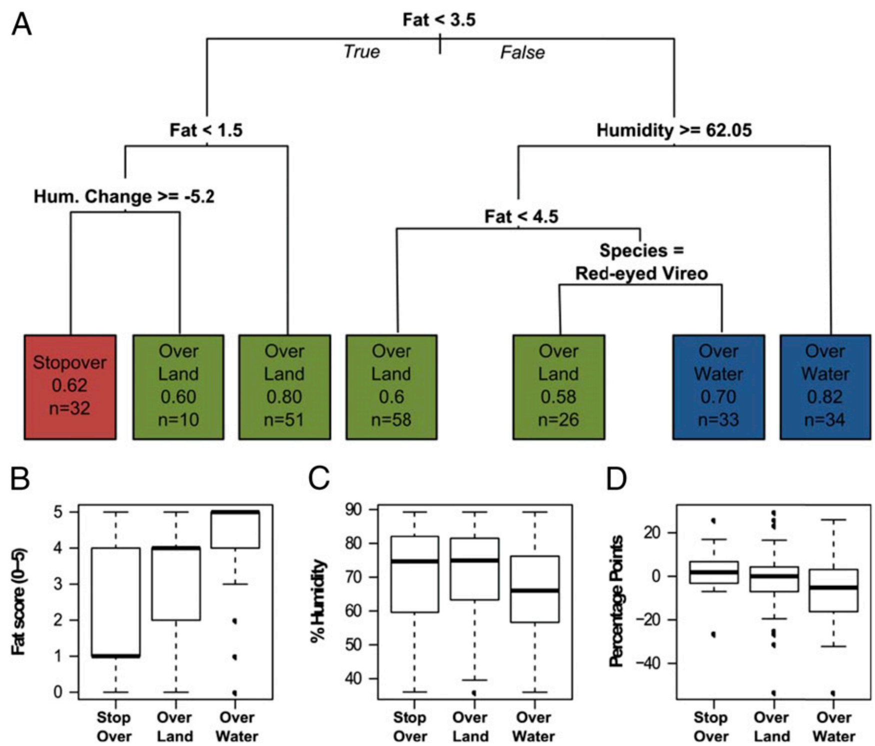

Fig. 3. (*A*) Classification and regression tree illustrating predicted classification of birds' departure decisions: stopover at coastal AL site for ≥24 h, over-land departure, or over-water departure. Box plots illustrate median and quartiles for variables predicting departure decision from AL: (*B*) fat scores, (*C*) humidity, and (*D*) 24-h change in humidity at sunset on the evening of capture. Negative values for change in humidity denote a drop in humidity, whereas positive values denote an increase in humidity. Sample sizes refer to number of individuals predicted in each class and the proportion reflects the accuracy of classification to each departure group.

Discussion

Our findings support the hypothesis that flexible strategies are adaptive for mitigating the dynamic conditions and risks of ecological barriers during migration (4, 24, 46). This study also advances our understanding of the interactions among intrinsic and extrinsic factors influencing decisions made by small songbirds to navigate potentially risky flights across the GOM. Songbirds departing from coastal Alabama were able to assess departure conditions to take advantage of favorable circumstances for crossing the Gulf safely and quickly.

Previous songbird data in support of this hypothesis along the edges of large geographic features have only considered either departure or arrival behavior (20, 31, 40, 41, 47), and the proximate cues and decision rules used to identify favorable conditions have been unclear (40). By detecting songbirds after negotiating ∼1,000 km of open water, we identified conditions affecting both departure and arrival, providing strong empirical support for the hypothesis that conditions that affect departure also influence crossing behaviors. We also identified criteria, or cutoff values, which may define birds' decision rules. In particular, fat, humidity, and wind profit are the proximate factors associated with movements across the GOM to the YP. The tight relationship between trans-Gulf (direct) flight durations and wind profit over the GOM further emphasizes the advantages accrued by exploiting favorable environmental conditions.

For the species we studied, fat score was the primary variable related to departure decision and arrival at the YP, suggesting that the amount of fat a bird carries is a key determinant of successful crossing. Birds departing the northern Gulf coast with large fat reserves have a larger buffer for dealing with en route exigencies, such as deteriorating weather conditions over open water, thereby improving their probability of arrival at the YP (31). Thus, birds may exert some control over their ability to mitigate risk associated with crossing the Gulf by increasing fat reserves before departure, provided they can locate and acquire food resources (48, 49). The importance of fat in shaping departure behavior (direction and stopover duration) at other coastal sites and islands suggests that our findings are applicable to migration across other geographic features (31, 47).

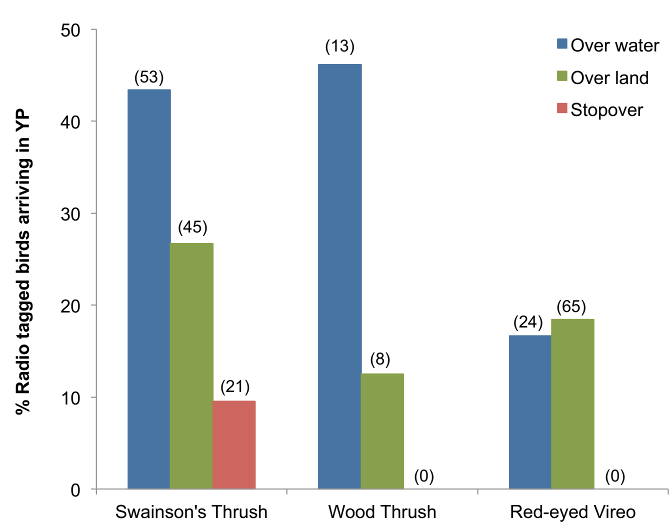

Fig. 4. Percentage of radio-tagged birds in each departure category that were detected in the Yucatan Peninsula. Sample sizes for each departure category within each of the three focal species are noted above bars.

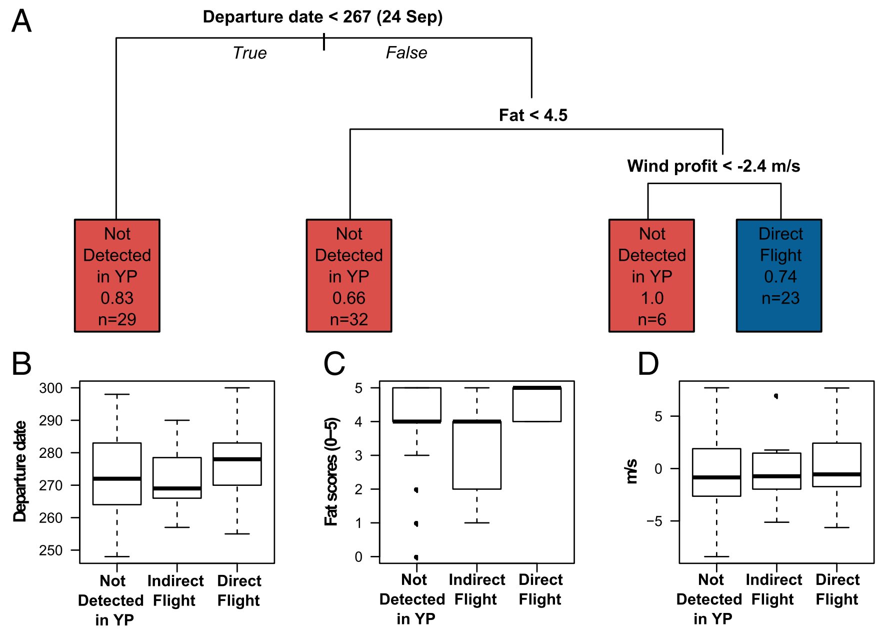

Fig. 5. (*A*) CART illustrating classification of birds among three arrival groups: birds that were not detected in the YP and those that arrived via indirect (>70 h following departure) and direct flights (<35 h following departure). Our CART of arrival at the YP includes only birds that departed over water on the evening of capture. Box plots illustrate median and quartiles for variables predicting arrival at the YP: (*B*) departure ordinal date, (*C*) fat score, and (*D*) wind profit. Positive wind-profit values denote headwinds, whereas negative values denote tailwinds. Larger-magnitude values indicate stronger wind speeds. Weather variables were retrieved for the date and time of departure.

The importance of fat in shaping both departure decisions and detection of over-water departures at the YP also underscores the value of high-quality habitat along the edge of geographic features that offer few, if any, refueling opportunities. In coastal areas, where human impacts are high, foraging opportunities may be reduced, limiting birds' ability to gain sufficient fat for nonstop flights over water (50). Birds do not gain mass at our capture site in AL (51), and a large percentage of lean birds depart the site over land (20), supporting the hypothesis that limited foraging opportunities along the coast may affect birds' likelihood of crossing the Gulf. Though interior sites may offer suitable refueling options for birds arriving at the coast with insufficient fat for crossing, our findings suggest that birds departing over land require significantly longer to arrive at the YP (vireos) or have a lower probability of arriving at the YP (thrushes) than birds departing over water.

Although extremely important, energetic reserves alone did not explain differences in migratory behaviors. Low humidity, wind profit (tailwinds or light headwinds), and ordinal day also were associated with songbirds' departure decisions from coastal AL as well as whether and when over-water departing birds arrived at the YP. Low (and dropping) humidity, clear skies, cooler temperatures, and southward winds are typical following the passage of a cold front (36). The tailwinds associated with this synoptic weather pattern are particularly valuable to migrants crossing the Gulf, because they increase ground speed and reduce travel time and energy expenditure (36, 38, 52). Additionally, the clear skies of low-humidity nights provide good visibility for departure orientation; clear skies correlate with more departures and less orientation scatter (53). Ordinal day is likely important for predicting the arrival of over-water departures because synoptic weather systems favoring trans-Gulf flights (i.e., strong cold fronts moving into the GOM) become more common later in the fall (late September through October) (19, 27, 54). The fate of birds departing over water before September 24 is unknown; they may have died due to unfavorable conditions or passed through other areas of the southern Gulf Basin.

Our study capitalized on our ability to detect small songbirds in the YP following their departure from coastal AL to provide insight into the factors and conditions that minimize risk of crossing the GOM and influence its role as an ecological barrier. We were unable to determine the fate of birds that were not detected in the YP, but it is expected that this subset of birds includes some radio-tagged individuals that successfully arrived elsewhere in the southern Gulf Basin, e.g., Cuba, and do not solely represent birds that died. This conclusion is supported by the overlap in the range of departure dates, fat, and wind profit between birds that arrived at the YP following trans-Gulf flights and those not detected in the YP (Fig. 5 *B*–*D*). It is reasonable to expect that similar conditions (e.g., large fat reserves, wind profit in the direction of travel to those areas) contribute to their ability to negotiate the GOM to arrive elsewhere.

Against our prediction, age appeared unrelated to the decision-making process. Provided young birds have sufficient fat and depart over water under favorable conditions, their likelihood of arrival at the YP, crossing times, and trans-Gulf flight durations are indistinguishable from those of adult birds, demonstrating that they are able to manage the risks associated with the GOM the first time then encounter it. Young and adult birds also are equally likely to cross the GOM in the spring (34). In contrast to our findings, young songbirds making short (average 35–65 km) migratory flights across water and along coastlines in New Brunswick, Canada, had longer flight durations than adults, because they departed under a broader range of wind conditions, including less-supportive winds (55). The lack of selectivity in departure conditions by young birds in New Brunswick may allow them to depart the breeding area quickly, providing benefits such as reduced exposure to predators, cold temperatures, and resource competition that outweigh energy and time savings associated with waiting for favorable winds (55). However, for birds crossing large water features like the GOM, the energy costs and mortality risk of crossing under less-profitable winds likely exert a much greater selection pressure on departure behavior, restricting the range of weather conditions under which migrants depart.

The similar response of young and adult birds in the GOM may be due to innately programmed decision rules, experience gained before arrival at on the northern coast of the GOM, or both.

Species differed in their migratory behaviors. Thrushes that initially departed over water had a higher probability of detection in the YP than birds departing over land or stopping over in coastal AL. In contrast, vireos had a similar likelihood of detection in the YP regardless of whether they departed the capture site over water or over land. This finding suggests that vireos did not have suitable conditions for traveling to the YP directly from the AL site, but were able to locate appropriate conditions elsewhere that allowed them to arrive at a later date. An important implication of this finding is that departure direction from a stopover site may not be a reliable indicator of a bird's endpoint or route, as many vireos departed to the north, a seasonally inappropriate direction, yet were detected in the YP.

In general, REVI negotiated risk associated with the GOM differently than the two thrush species, which responded similarly. The GOM may function more as a barrier to vireos. Vireos departed over land more frequently than thrushes, likely in response to greater constraints in the weather conditions permitting over-water departure (specifically humidity), had a lower overall likelihood of arrival at the YP, took almost seven times longer to cross the Gulf, and had arrival patterns that were less influenced by departure decisions. The differences between vireos and thrushes are not explained by initial fat reserves, biogeography, or flight morphology. Mean fat scores of vireos were significantly higher than those of SWTH but similar to those of WOTH (*SI Methods*, Fig. S5). Previous studies have shown that REVI and SWTH captured in coastal AL with large fat reserves orient toward South America (28, 56), and geolocator studies confirm that both species moving through the northern coast of the GOM arrive at South American winter grounds (23, 57). Based on differences in species' flight morphologies (wing loadings and aspect ratios), vireos are expected to be more energy-efficient during long-distance flights than either thrush species, particularly WOTH (58, 59), and less susceptible to weather effects (9); thus we expected the GOM to represent less of a barrier to vireos. An alternative explanation is that the smaller body size of vireos translates into slower airspeeds (38) and consequently longer flights and a greater probability of exposure to inclement weather; however, our comparison of trans-Gulf flight times demonstrated no difference among species.

Wintering ecology, diet, and habitat requirements may explain the differences observed in the species migratory behavior. REVI winter in mixed-species flocks and are not territorial (60, 61); thus, their arrival time may be less constrained, allowing them to wait for more favorable conditions and avoid the risks of crossing a large body of water. Conversely, SWTH and WOTH defend winter territories (62, 63), and the benefits of taking quicker, more direct routes to acquire higher quality territories may outweigh the potential risk of encountering inclement weather over water. Additionally, although all three species are known to consume fruit during fall migration and on the wintering grounds, REVIs typically glean insectivorous prey from broad-leaved canopy foliage (48, 64, 65), whereas Swainson's Thrush and Wood Thrush forage on the ground and in low vegetation (66, 67). The scrub-shrub and pine vegetation along the Fort Morgan (FTM) Peninsula may be more at odds with vireos' broad-leaved canopy foraging preferences than the understory preferences of the thrush species. REVIs may have departed over land in search of vegetation better suited to their foraging habits.

During migration, birds encounter and respond to spatiotemporally fluctuating landscapes. Consequently, they are constantly assessing risk by comparing alternative behaviors, whether it be when or where to land, in which vegetation type to settle, which food resources to consume, or when and in what direction to depart from a stopover site to minimize fitness costs. A major finding of this study is that songbirds encountering the GOM appear to mitigate risk in relation to crossing the Gulf by departing with large fat reserves when weather variables signal favorable flight conditions. Birds have some control over fat gain and can decide when and in which direction to depart when facing different weather conditions. By adjusting their behaviors, they can exert some control over the extent to which the GOM functions as a barrier and inhibits or facilitates safe, timely, and energy-efficient movement toward their wintering destinations.

Materials

Capture and Tagging Methods. We captured, radio-tagged, and gathered intrinsic measurements (age, wing chord length, fat score) on Red-eyed Vireos, Swainson's Thrushes, and Wood Thrushes at a long-term banding station in the Bon Secour National Wildlife Refuge (30° 13′ 49″ N, 88° 0′ 13″ W) on the FTM Peninsula, AL, from September 2 to October 28, 2009–2013. The FTM Peninsula is located directly south of Mobile Bay along the northern coast of the GOM (Fig. 1, *SI Methods*, Fig. S1). We fitted analog pulse transmitters to birds using a modified adhesive approach (20, 68) (*SI Methods*).

Automated Tracking in the GOM. We operated three automated radio-tracking towers along the coast within 7.5 km of our AL capture site each season (*SI Methods*, Fig. S1). We mounted six 3-element directional Yagi antennas at 60° intervals on each tower to estimate birds' departure direction in degrees and classify departures as over water or over land (69, 70). In 2012 we added a tracking tower to Dauphin Island (7.5 km west of capture site), and in 2013 we added a tower to the north of Mobile Bay; the latter was equipped with four high-gain, stacked directional antennas to improve detection of birds that departed over land. We used automated receiving units (JDJC Corp.) to autonomously monitor transmitter frequencies at 0.5- to 4-min intervals.

We established a "telemetry fence" along the entire northern coast of the YP using seven tracking towers, each equipped with high-gain stacked antennas identical to the ones used in AL (Fig. 1). We oriented two high-gain antennas toward 90° and 270°, roughly parallel to the northern YP coastline, to detect radio-tagged birds as they arrived. We spaced towers an average of 57 ± 7 km (±SD) apart along the YP coast to maintain continuous detection. We sampled each transmitter frequency at 3-to 6-min intervals in the YP.

Departure and Arrival Date, Time, and Direction. We conservatively detected radio-tagged birds in AL and the YP based on signal strength, background noise, pulse width, pulse interval, measured frequency, and temporal pattern of detections (71) (*SI Methods*). In AL, when sufficient data were available from multiple towers, we used biangulation or triangulation to estimate each bird's departure direction and time based on the last five track coordinates (20). When insufficient data were available for track estimation, we estimated vanishing bearings based on changes in signal strength across the six antennas of the strongest tower. We used the last detection to estimate departure bearing and time. Stopover duration was conservatively estimated as the difference between capture date and date of departure determined by our telemetry data. When a bird was detected in the YP, we estimated arrival time as the time of peak signal strength on the east or west antenna of the strongest tower. Departure and arrival data are archived in Movebank (72).

Weather Data. We retrieved weather variables from the National Center for Environmental Prediction North American Regional Reanalysis dataset (73) via the Environmental Data Automated Track Annotation System (Env-DATA) service available on www.movebank.org (72, 74). Variables were interpolated to the nearest time, location, and altitude. We examined correlations among weather variables and only retained variables with $|r| < 0.60$ (Tables S1 and S2). We retrieved the following variables predictive of synoptic weather systems: (*i*) surface-level humidity; (*ii*) surface-level barometric pressure; (*iii*) 24-h change in surface humidity (negative values indicate a drop in humidity, positive values an increase); (*iv*) 24-h change in surface pressure (sign denotes direction of change); (*v*) wind speed at four altitudes (1, 2, 3, and 4 km); and (*vi*) wind direction at four altitudes. We used wind speeds and directions to calculate an average wind-profit index. Wind profit was defined as the speed (m/s) of wind toward 180° (i.e., how favorable winds were for crossing to the YP; see formula for wind profit in ref. 46). Positive wind-profit values denote favorable winds for crossing to the

YP (i.e., tailwinds), whereas negative values denote unfavorable winds (i.e., headwinds). Larger-magnitude values indicate stronger wind speeds. For the CART analyses we calculated an average wind profit across the four altitudes at the capture site at civil twilight or the time of birds' departure. For the analysis of trans-Gulf flight duration we calculated a Gulf-wide wind-profit index by averaging conditions across the four altitudes along a simulated track beginning at civil twilight with a track direction of 180° and assuming a constant heading (*SI Methods*).

Statistical Analyses. We used GLMM with a multinomial distribution and generalized logit link function to examine differences in departure decisions among species and to assess patterns of arrival (direct flight, indirect flight, not detected) in relation to species and departure decision. We modeled departure day as a random effect to account for potential nonindependence of multiple individuals departing on the same day.

We performed a CART analysis to determine which extrinsic and intrinsic factors predicted each of the three departure decisions in AL: over-water departure, over-land departure, or stopover (75). Model predictors included species, fat score (0–5) (76), age, relative wing length (*z*-score, calculated within each species), ordinal date, relative humidity, 24-h change in humidity, barometric pressure, 24-h change in pressure, and wind profit at civil twilight on the date of capture to objectively compare weather available to birds that departed on the evening of capture and those that did not (*SI Methods*). Most migrants depart at civil twilight and likely decide whether to depart based on conditions at that time (20).

We performed a second CART analysis to determine which factors were related to the detection of over-water departing birds in the YP, distinguishing between birds that arrived following a direct, trans-Gulf flight and those arriving >70 h after departure from AL, either via a delayed trans-Gulf flight or a detour around the Gulf. We restricted this analysis to birds that departed over water on the day of capture, because they were the only birds for which we had reliable fat scores and weather conditions at the time of departure and because the departure behavior of these birds suggested they selected a trans-Gulf route. We classified over-water departures into one of three groups: direct flight, indirect flight, and nonarrival. All predictors were the same as in the departure decision analysis, except that we used weather conditions at the actual time of birds' departure.

We performed a GLMM with a negative binomial distribution and a log-link function to compare stopover duration among species and predict crossing time (represented as number of hours) as a function of intrinsic and extrinsic variables. We modeled departure day as a random effect to account for multiple individuals departing on the same day. For trans-Gulf flight duration, we used a GLM with a negative binomial distribution and log-link function but omitted the random effect of date because of difficulty fitting the full model due to the small sample size. Single-variable GLMM for trans-Gulf flight duration with the random effect of date produced qualitative results identical to the full model without date. We computed all statistics in R 2.15.2 (package rpart; *SI Methods*) or SAS 9.4 (PROC GLIMMIX).

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