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Cite this article: Ward MP, Benson TJ, Deppe J, Zenzal Jr TJ, Diehl RH, Celis-Murillo A, Bolus R, Moore FR. 2018 Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration. *Proc. R. Soc. B* **285**: 20181747.
http://dx.doi.org/10.1098/rspb.2018.1747

Received: 7 August 2018
Accepted: 27 September 2018

Subject Category:
Ecology

Subject Areas:
ecology, behaviour

Keywords:
migration, geographical barriers, survival, wind profit, fat stores, Swainson's thrush

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Electronic supplementary material is available online at https://dx.doi.org/10.6084/m9.figshare.c.4258196.

THE ROYAL SOCIETY PUBLISHING

Estimating apparent survival of songbirds crossing the Gulf of Mexico during autumn migration

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Many migratory bird species are declining, and the migratory period may limit populations because of the risk in traversing large geographical features during passage. Using automated radio-telemetry, we tracked 139 Swainson's thrushes (*Catharus ustulatus*) departing coastal Alabama, USA and crossing the Gulf of Mexico to arrive in the Yucatan Peninsula, Mexico during autumn. We estimated apparent survival and examined how extrinsic (weather variables and day of year) and intrinsic (fat load, sex and age) factors influenced survival using a mark-recapture approach. We also examined how favourability of winds for crossing the Gulf varied over the past 25 years. Fat load, day of year and wind profit were important factors in predicting which individuals survived crossing the Gulf. Survival estimates varied with wind profit and fat, but generally, fat birds departing on days with favourable wind profits had an apparent survival probability of greater than 0.90, while lean individuals with no or negative wind profits had less than 0.33. The proportion of favourable nights varied within and among years, but has increased over the last 25 years. While conservation strategies cannot improve extrinsic factors, they can provide opportunities for birds to refuel before crossing large geographical features through protecting and creating high-quality stopover sites.

1. Introduction

Migratory animals, regardless of taxa, are declining [1]. Birds, specifically, face growing challenges during migration, including loss of stopover habitat [2], changes in climate [3] and potential collisions with tall, man-made structures like wind turbines [4] and skyscrapers [5]. Even without these hazards, migration is a challenging period in the annual cycle of many bird species. Migrating birds must find suitable stopover habitat, avoid predators, quickly replenish fat stores and make appropriate decisions in response to weather conditions, all while advancing towards their destinations [6]. Moreover, large, inhospitable geographical features figure prominently in the movement ecology of almost all long-distance migratory birds throughout the world (e.g. Sahara Desert [7], North Sea [8] and Atlantic Ocean [9]). A geographical feature that may present an obstacle for migration of many Nearctic–Neotropical migratory birds is the Gulf of Mexico [10]. Reports of landbirds resting on offshore oil and gas platforms [11], washing ashore in large beach kills [12] and being found in shark stomach contents [13] support that crossing large water bodies such as the Gulf of Mexico poses a risk. However, accepting the potential risks, large geographical features, such as the Gulf of Mexico, may provide corridors allowing individuals to more quickly and safely reach their destination [14].

Although migration is thought to be the most hazardous phase of the avian annual cycle [12,15,16], robust estimates of survival during migration are few [15]. The lack of season-specific survival estimates is primarily owing to the logistical and technological difficulties of gathering data needed to produce robust estimates, especially for small birds during the migratory period. Furthermore, mortality during migration is probably not evenly distributed along the migratory route. Large geographical features like the Gulf of Mexico may have a disproportionate impact on survival. While knowledge of average season-specific survival rates during the annual cycle can assist in conserving migratory bird populations, identification of specific migratory events that exert the greatest influence on survival will focus conservation efforts on areas of greatest importance. Indeed, information is needed to better understand when and where populations become limited during migration, as well as to inform management and conservation efforts [2].

The role that the Gulf of Mexico plays in the survival of small land birds during autumn migration is expected to be dynamic. The greater than 1000 km crossing between the northern Gulf Coast and the Yucatan Peninsula (YP) in autumn requires, on average, 22 h of sustained flight for land birds such as Swainson's thrush (*Catharus ustulatus*) [17]. Relative to spring, autumn crossing poses unique challenges, including greater likelihood of encountering unfavourable winds [18] and young birds crossing for the first time. Extrinsic factors such as weather and intrinsic factors such as age, sex and fat stores influence survival when crossing large geographical features [7,17]. The ability to determine the favourability of winds and respond accordingly should be adaptive [19,20]; both wind speed and direction should strongly influence whether an individual attempts to cross a large geographical feature [17]. The fat stores that individual birds accumulate before departure are an important determinant of stopover duration for spring- and autumn-migrating birds [21–23], influence departure decisions [17,20,24–26] and surely influence the duration of their migratory flights [27]. Age may also contribute to an individual's probability of survival *en route* across large geographical features such as the Gulf of Mexico because young birds crossing for the first time may have a lower survival probability than older, experienced individuals [28,29]. Finally, the sex of an individual may influence survival if males experience greater pressure to return early to wintering grounds [30] or because sexually dimorphic wing shape influences flight performance in relation to atmospheric conditions [31]. From a conservation perspective, it is important to consider not only relationships between survival and extrinsic variables, but also how conditions for crossing the Gulf of Mexico varied in the past and are forecast to change in the future, as climate change alters the frequency and strength of favourable winds [32]. Assessing whether these changes will be beneficial or detrimental to migratory birds requires a better understanding of how birds respond to and are influenced by wind when negotiating large geographical features.

We estimated the apparent survival of Swainson's thrushes as they attempted to cross the Gulf of Mexico during autumn migration. Swainson's thrushes are well suited for examining trans-Gulf survival as most individuals probably cross on their way to wintering grounds in South America and are large enough to carry a small transmitter [17]. Additionally, the species' migratory behaviour has been studied for decades [17,28,33–35]. Previous research has shown that Swainson's thrushes typically fly for 7 h each night during overland flights [33,36] and an average of 22 h over the Gulf [17]. Thus, crossing of the Gulf of Mexico requires a prolonged flight three times greater than their average migratory flight over land. We were able to directly monitor the departure of radio-tagged Swainson's thrushes leaving the Alabama coast (northern coast of the Gulf of Mexico) and their arrival at the YP (southern coast of the Gulf of Mexico) using a network of automated radio-telemetry systems (ARTS). We set out to address: (i) how extrinsic (weather and day of year) and intrinsic (fat, age and sex) factors influence survival of Swainson's thrushes crossing the Gulf of Mexico during autumn passage, and (ii) how the favourability of weather conditions for crossing the Gulf of Mexico has changed over the past 25 years.

2. Material and methods

(a) Study species

We captured and radio-tagged Swainson's thrushes at a long-term banding station in the Bon Secour National Wildlife Refuge (30°13′49″ N, 88°0′13″ W) on the Fort Morgan (FTM) Peninsula, Alabama, USA. Mist-nets were in operation from 2 September to 28 October 2009–2014. We generally operated mist-nets between sunrise and noon, unless unfavourable weather prohibited their safe operation. We banded each bird with a uniquely numbered United States Geological Survey aluminium band. We classified birds as hatch year (HY) or after-hatch year (AHY) based on plumage characteristics and skull pneumatization [37]. We assigned all birds a fat score ranging from 0 to 5 based on visible subcutaneous fat [38]. We used each bird's fat score as an index of its physical condition [39]. We determined an individual's sex genetically using feathers collected from the individuals (Animal Genetics, Tallahassee, FL, USA).

Thrushes were tagged with analogue, pulse transmitters from JDJC Corp., (Fisher, IL, USA). Each transmitter had a unique frequency between 163.828 and 166.060 MHz, had pulse width (i.e. the duration of the radio pulse) of either 22 ± 2 or 28 ± 2 ms ($\pm$s.e., manufacturer specified) and a pulse interval of 350 ± 10 ms. We attached transmitters to birds dorsally between the wings with an eyelash adhesive (Revlon® brand) and a small amount of cyanoacrylate glue (Loctite® brand) [40]. Transmitters weighed ~1.1 g with cloth and thread, and had a lifespan of approximately 28 days. Transmitters weighed less than 5% of each bird's body mass and, in most cases, less than 3%. No individuals were captured between years.

(b) Automated tracking data

An ARTS network consisting of four receiving towers was operated on the FTM Peninsula to estimate the departure date, time and direction for each bird (figure 1*a*) and seven ARTS across the northern tip of the YP to record the arrival in the Yucatan (figure 1*b*). The precise locations of the towers on the FTM Peninsula used in this study changed slightly among years depending on site access, although two towers were always within 1.8 km of the banding station. We were able to detect all departures from the study area.

To detect the arrival of birds in Mexico, we established a 'telemetry fence' along the northern coast of the YP using seven ARTS (figure 1*b*), each equipped with two high-gain stacked Yagi antennas. The high-gain antennas were oriented towards the east (90°) and west (270°). All antennas were erected above the vegetation and other surrounding objects approximately 10.6 ± 2.4 m above

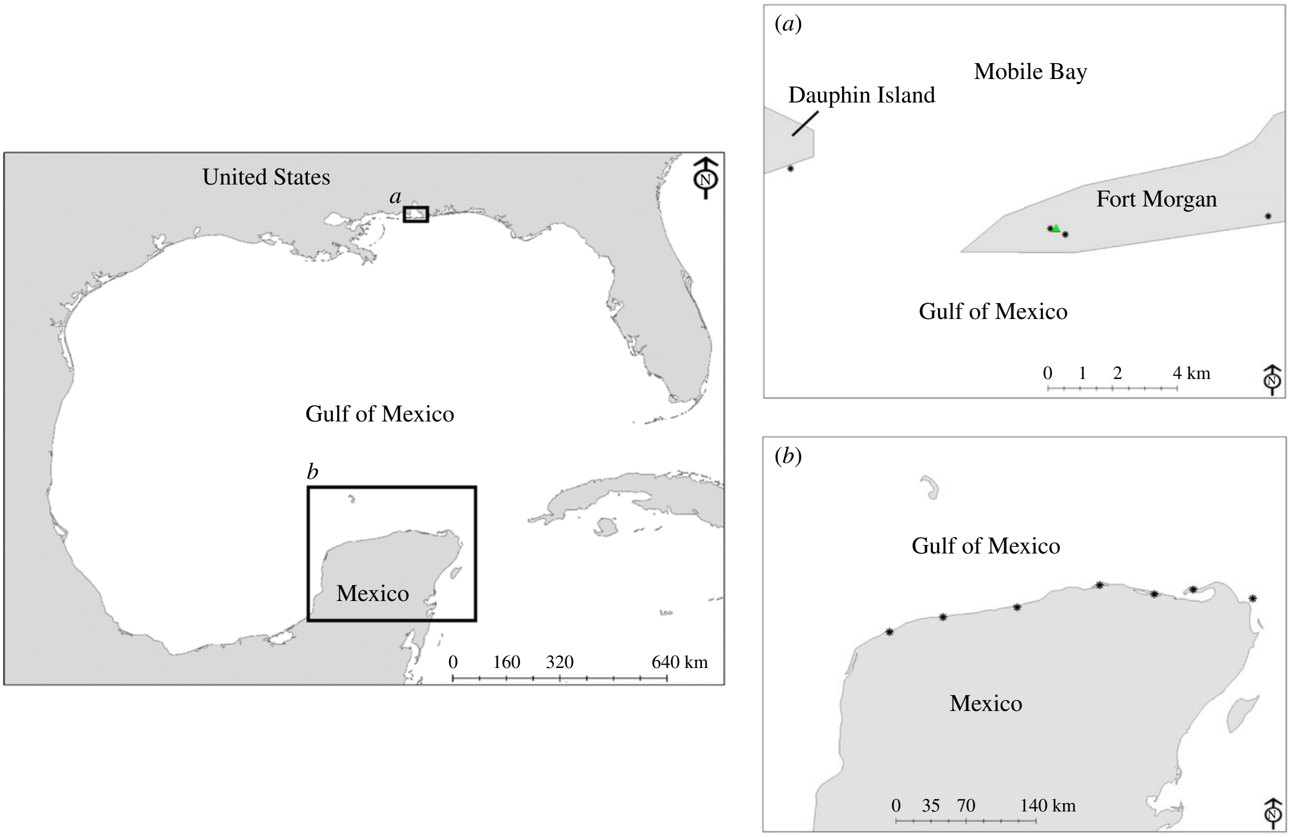

Figure 1. Locations of the ARTS used to track both the departure of migratory birds from the northern coast of the Gulf of Mexico and their subsequent arrival at the YP. (*a*) Locations of ARTS (asterisks) and banding station (green triangle) on the Alabama coast. (*b*) Location of ARTS along the coast of the YP.

ground level to improve the detection capabilities of our tracking towers. The flat topography of the northern YP favoured the detection of arriving birds by our tracking towers (assuming transmitters were still functioning); and the fact that, in most instances, arriving birds were detected almost simultaneously on multiple towers suggests we were able to detect all radio-tagged birds passing through the northern YP. Towers in the YP were separated by an average 42 km. The maximum range of detection of a radio-tagged bird is largely determined by the bird's altitude (in relation to offsetting the effect of the Earth's curvature to achieve line-of-sight contact), transmitter power, receiving antenna gain and orientation of the transmitting antenna with respect to the receiving antenna. Theoretically, a bird flying at an altitude of 500 m above sea level could be detected at a range of 80 km using our high-gain antennas, while a bird flying at an altitude of 1000 m could be detected at a range of approximately 115 km [17]. While we do not know the exact altitude of birds arriving in the YP, previous studies suggest that most songbirds migrate at altitudes greater than 500 m above ground level [41]. The ARTS in the Yucatan experienced more periods in which they were not operating compared with Alabama, primarily owing to the occurrence of hurricanes. The percentage of time the automated receiving units were operating was: 2009—100.0%; 2010—97.4%; 2011—76.7%; 2012—94.2%; 2013—98.2%; 2014—100.0%. While some towers may not have been operating, 44% of birds detected in the Yucatan were detected on multiple towers. On average, a detected bird was detected on 1.91 towers and was detected for an average of 54.9 min (minimum 15.0 min–maximum 126.0 min). Also, most of the time when towers were not functional was early in season, while thrush migration was generally later in the season. Further information on the criteria used to identify the arrival of radio-transmittered birds in the YP can be found in the electronic supplementary material [17,42]. Information on calculating the departure directions can be found in the electronic supplementary material [25]. The detection history for these individuals is available at https://doi.org/10.13012/B2IDB-2805211_V1.

(c) Weather variables

We used weather variables from the National Center for Environmental Prediction (NCEP) North American Regional Reanalysis (NARR) dataset [43]. We obtained NARR variables from the Environmental Data Automated Track Annotation System (Env-DATA) service available on Movebank.org, a website repository of animal movement data [43–45]. The Env-DATA service provides interpolated variables to the nearest time, location and altitude using an inverse distance weighted method. NARR has 3 h temporal resolution, 32 km horizontal resolution and approximately 250 m vertical resolution.

We only considered weather variables found to influence migration behaviour in birds [17,26] including relative humidity, barometric pressure, precipitation, temperature, and wind speed and direction (the latter two were calculated from the u- and v-wind vector components). For our purposes, wind direction refers to the direction towards which the wind is moving. We used wind speeds and directions to calculate a wind profit index. Wind profit was defined by the favourability of winds for crossing to the YP, or specifically as the speed ($m\ s^{-1}$) component of wind towards 180° (south). Cross winds have also been found to be important in the behaviour of migrants [19,46]; therefore, we also included the magnitude of cross winds (u-wind vector component) in our analyses. Because we had no *a priori* reason to expect different effects of easterly versus westerly winds, we used the absolute value of the u-wind component (although using the original values gave qualitatively and quantitatively similar results). We created a model to simulate the track across the Gulf and the conditions experienced by migrating birds; details can be found in the electronic supplementary material.

(d) Survival analyses

We estimated apparent survival using robust-design models in program MARK [47–49] (see the electronic supplementary

Table 1. Candidate models used to examine the influence of intrinsic and extrinsic factors influencing apparent survival (φ) of Swainson's thrushes (*Catharus ustulatus*) crossing the Gulf of Mexico during autumn migration, 2009–2014. (Models were robust-design mark-recapture models that account for imperfect detection (p) and temporary emigration from our automated telemetry system (γ'' = probability of emigrating; γ' = probability of staying away given prior emigration). Variables listed in parentheses represent the covariate structure used to model variation in each parameter; periods represent parameters with no covariates. South represents the birds that departed between 160° and 220°.)

model	K	ΔAIC_c	AIC_c	w_i
φ(south + fat + dep. date^2 + wind profit + (south × wind profit)) γ''(.) γ'(.) p(cap. date + fat)	12	0	689.74	0.91
φ(south + fat + dep. date^2 + crosswinds + (south × crosswinds)) γ''(.) γ'(.) p(cap. date + fat)	12	7.48	697.22	0.02
φ(south + fat + dep. date^2 + precip. + (south × precip.)) γ''(.) γ'(.) p(cap. date + fat)	12	7.61	697.35	0.02
φ(south + fat + dep. date^2) γ''(.) γ'(.) p(cap. date + fat)	10	9.50	699.24	0.01
φ(south + fat + dep. date^2 + wind profit) γ''(.) γ'(.) p(cap. date + fat)	11	9.90	699.63	0.01
φ(south + fat) γ''(.) γ'(.) p(cap. date + fat)	8	9.93	699.66	0.01
φ(south + fat + dep. date) γ''(.) γ'(.) p(cap. date + fat)	9	11.03	700.77	<0.01
φ(south + fat + dep. date^2 + temperature) γ''(.) γ'(.) p(cap. date + fat)	11	11.05	700.79	<0.01
φ(south + fat + dep. date^2 + rel. humidity) γ''(.) γ'(.) p(cap. date + fat)	11	11.08	700.81	<0.01
φ(south + fat + dep. date^2 + precipitation) γ''(.) γ'(.) p(cap. date + fat)	11	11.15	700.89	<0.01
φ(south + fat + dep. date^2 + crosswinds) γ''(.) γ'(.) p(cap. date + fat)	11	11.25	700.99	<0.01
φ(south + fat + dep. date^2 + pressure) γ''(.) γ'(.) p(cap. date + fat)	11	11.50	701.24	<0.01
φ(south + fat + (south × fat)) γ''(.) γ'(.) p(cap. date + fat)	9	11.98	701.71	<0.01
φ(south + fat + dep. date^2 + temperature + (south × temperature)) γ''(.) γ'(.) p(cap. date + fat)	12	12.07	701.81	<0.01
φ(south + fat + dep. date^2 + pressure + (south × pressure)) γ''(.) γ'(.) p(cap. date + fat)	12	12.59	702.33	<0.01
φ(south + fat + dep. date + (south × dep. date)) γ''(.) γ'(.) p(cap. date + fat)	10	13.02	702.76	<0.01
φ(south + fat + dep. date^2 + rel. humidity + (south × rel. humidity)) γ''(.) γ'(.) p(cap. date + fat)	12	13.15	702.89	<0.01
φ(south + fat + dep. date^2 + (south × dep. date^2)) γ''(.) γ'(.) p(cap. date + fat)	12	13.30	703.04	<0.01
φ(south) γ''(.) γ'(.) p(cap. date + fat)	7	17.44	707.18	<0.01
φ(.) γ''(.) γ'(.) p(cap. date + fat)	6	17.82	707.56	<0.01
φ(south + age) γ''(.) γ'(.) p(cap. date + fat)	8	18.56	708.30	<0.01
φ(south + sex) γ''(.) γ'(.) p(cap. date + fat)	8	18.68	708.42	<0.01
φ(south + age + (south × age)) γ''(.) γ'(.) p(cap. date + fat)	9	20.29	710.03	<0.01

material for details on how the detection histories were generated). Before examining the influence of covariates on apparent survival, we first evaluated their influence on detection (resighting) probability (p), and the two emigration parameters: γ'' = probability of emigrating and γ' = probability of staying away given prior emigration. Using Akaike's information criterion (AIC_c; [50]), we evaluated the potential influence of age, sex, fat score, and linear and quadratic effects of capture date; we carried forward the best-fitting covariate structure for these parameters to our evaluation of factors influencing apparent survival. Because our data structure functionally included a single secondary period for the YP, our models assumed similar detection probability in Alabama and YP (see estimates below) for individuals that both survived and did not permanently emigrate from our system. Our criteria for classifying detections of individuals ([18], and above) confirmed that detection probability was high on our YP system. Fat score was only available on the day of capture; hence, the fat scores of a few birds ($n = 13$ out of 139 tagged birds) that did not immediately depart south may have changed. To examine apparent survival, we focused on birds departing in a southward direction as we considered these individuals as most probably attempting a trans-Gulf flight. We created a dichotomous variable for birds either departing south (between 160° and 220°) or in other directions, and included this variable with intrinsic and extrinsic covariates in candidate models (table 1). Intrinsic covariates included age, sex and fat score, whereas extrinsic variables included temperature, relative humidity, barometric pressure, precipitation, wind profit and linear and quadratic effects of departure date. We parametrized models to estimate separate values for the small number of birds with unknown sex or age. We did not include year in the models because, from a biological perspective, we expected yearly variation owing to extrinsic and intrinsic factors, and we were more interested in these specific factors. Moreover, from an analytical perspective, adding year to the mark-recapture models as a fixed or random effect would probably result in overparametrization and problems with model convergence. To limit the number of potential candidate models, we first examined the effects of intrinsic covariates and departure date, and included the best-fitting intrinsic and date covariates in subsequent weather models. We expected values for south-departing birds to be most indicative of true survival of individuals attempting to cross the Gulf. Therefore, we also evaluated interactions between our south category and our variables of interest, with the rationale that effects of these covariates would only manifest for south-departing birds. We evaluated correlations among all of our explanatory variables prior to conducting analyses and did not include highly correlated variables

($|r| > 0.7$) together in any models (electronic supplementary material, figure S1 includes the correlation plots of variables).

(e) Frequency of favourable weather for migration

To examine the historical distribution of favourable days for migration across the Gulf of Mexico, we used the same nightly weather data as described above for 1990–2014. Specifically, we used our calculated values for wind profit from 1 September to 31 October of each year, along with the coefficients from our best-fit model for factors influencing apparent survival to generate predicted values for survival of Gulf crossing birds. Based on these results, we then examined whether there have been trends in the proportion of favourable nights for migration (defined as nights with predicted $\varphi \geq 0.80$) across years for birds in six different fat classes (0–5) using a generalized linear model (binomial distribution, logit link function). We examined the linear and quadratic effect of year, the effect of fat score and the potential interaction between year and fat score.

3. Results

We captured and radio-tagged 139 Swainson's thrushes (16–32 individuals per year) from 13 September to 28 October 2009–2014. Of these, there were 70 males and 58 females (11 of unknown sex); 91 were classified as young (HY) and 47 as adult (AHY) (one unknown). Fat scores ranged from 0 to 5 (mean = 3.08, s.d. = 1.78), with 55% ($n = 76$) classified as 4 or 5. Most birds ($n = 112$; 81%) departed FTM the same day of capture, and 9% ($n = 13$) stopped over for 3 or more days; 43 birds (31%) were redetected in the Yucatan.

Our AIC approach found the best model for detection (resighting) probability (p) included additive effects of capture date and fat score (table 1) with probability declining with capture date and increasing with fat score, and estimated detection probability per 6 h period ranged from 0.79 to 0.95, with an estimated probability of 0.91 ($\pm$0.01 s.e.) for a bird captured on 2 October with a fat score of 3. The best-fitting structure for our temporary emigration parameters (γ'' and γ') included no covariates, with an estimated probability of emigrating from our system (γ'') of 0.22 ($\pm$0.06 s.e.), and estimated probability of staying away given prior emigration (γ') of 0.78 ($\pm$0.06 s.e.).

Both intrinsic and extrinsic factors were well supported as predictors of survival (φ) for thrushes attempting to cross the Gulf of Mexico. The best-fitting model included positive influences of fat score and wind profit with the wind profit effect specific to south-departing individuals, and a quadratic effect of departure date (table 1). Estimated survival was highest for fat, south-departing birds on nights with favourable wind profit (positive values denote favourable tailwinds and negative values indicate headwinds; figure 2), and peaked around 8 October (figure 3). The estimated apparent survival for a south-departing individual leaving on 8 October (the average departure date) with a fat score of 5 was 0.80 ($\pm$0.09 s.e.) under average wind conditions (wind profit = $-0.7\ \mathrm{m\,s^{-1}}$); 0.91 ($\pm$0.06 s.e.) under favourable wind conditions (upper quartile for wind profit = $0.9\ \mathrm{m\,s^{-1}}$) and 0.98 ($\pm$0.02 s.e.) under the maximum observed wind profit ($4.4\ \mathrm{m\,s^{-1}}$). To illustrate the role of fat score, the apparent survival for an individual with a fat score of 1 was 0.29 ($\pm$0.16 s.e.), 0.49 ($\pm$0.21 s.e.) and 0.87 ($\pm$0.17 s.e.) under average, favourable and maximum wind profit, respectively. We found little support for effects of age, sex or other weather conditions on apparent survival.

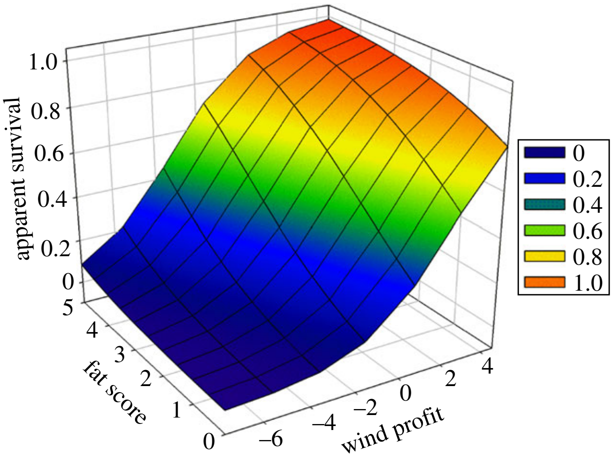

Figure 2. Predicted apparent survival for south-departing Swainson's thrushes (*Catharus ustulatus*) crossing the Gulf of Mexico on 2 October 2009–2014, as a function of fat score and wind profit. We generated estimates for 2 October because this was the average departure date for individuals in the study and the first week of October corresponds to the timing of peak arrival at this site based on long-term data (O. R. Woodrey, F. R. Moore 1997, unpublished data).

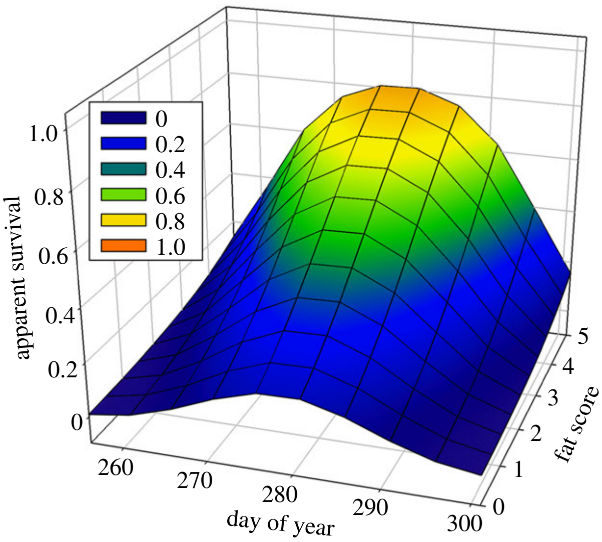

Figure 3. Predicted apparent survival for south-departing Swainson's thrushes (*Catharus ustulatus*) crossing the Gulf of Mexico during autumn migration under average wind conditions (wind profit = $-0.7\ \mathrm{m\,s^{-1}}$), 2009–2014, as a function of fat score and day of year.

Wind profit varied considerably within and among years. Across all years (1990–2014), wind profit during September and October ranged from -25.0 to $11.5\ \mathrm{m\,s^{-1}}$ with a mean of -1.8 (s.d. = 4.1). Annual mean values for wind profit ranged from -4.3 (1998) to $-0.1\ \mathrm{m\,s^{-1}}$ (2005). Similarly, there was considerable variation within and among years in the number and distribution of nights when conditions would be expected to be favourable ($\varphi \geq 0.80$) for trans-Gulf migration (figure 4). The was no evidence that the proportion of favourable nights for crossing the Gulf changed differently over time for birds in different fat classes (fat × year: $F_{5,138} = 0.56$, $p = 0.732$), so we dropped the interaction to evaluate the influence of the main effects. The proportion of favourable nights for crossing within each autumn migration season increased from 1990 to 2014 (electronic supplementary material, figure S2; year: $F_{1,143} = 4.04$, $p = 0.046$; $\beta = 0.0059$,

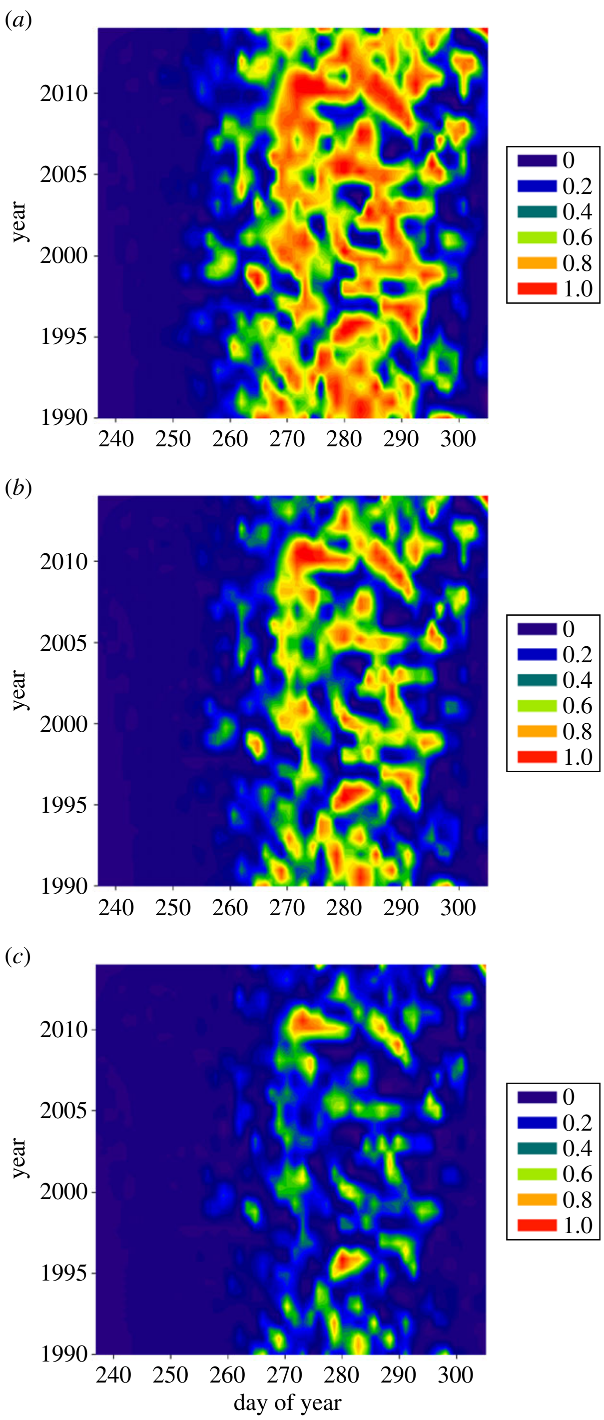

Figure 4. Predicted apparent survival for Swainson's thrushes (*Catharus ustulatus*) attempting to cross the Gulf of Mexico during autumn migration with high (*a*; fat score = 5), moderate (*b*; fat score = 3) or poor fat stores (*c*; fat score = 1) as a function of day of year and calculated nightly wind profit for the years 1990 through to 2014.

95% confidence interval (CI) 0.0001–0.0118), although there was no evidence of a quadratic effect (year^2: $F_{1,142} = 1.52$, $p = 0.219$).

4. Discussion

The risk to Swainson's thrushes crossing the Gulf of Mexico in autumn is closely tied to the individual's fat stores, wind direction and wind speed. Under ideal conditions, crossing poses little risk to the individual, but under less than favourable conditions, the crossing might be one of the riskiest events of autumn migration and the annual cycle. Survival is unlikely if birds attempt to cross under strong headwinds, regardless of their fat stores. For lean birds, survival remains low even under favourable wind conditions (wind profit = 0.9). Of the 76 lean birds we tagged, only six departed towards the south, out over the Gulf, and only one was subsequently detected in the YP. That individual, however, spent 9 days in the capture area at FTM prior to departure and probably gained fat [28] before departing across the Gulf. While crossing the Gulf of Mexico under unfavourable conditions may be one of the riskiest events during autumn migration, birds presumably have evolved departure decision rules and sensitivity to environmental cues that maximize the probability of survival by coordinating trans-Gulf departures with favourable intrinsic and extrinsic conditions [18].

The apparent survival of thrushes crossing the Gulf was driven by factors birds have some capacity to manage: wind profit, fat load and day of year. Several studies have found that birds prefer to migrate when winds are in their favour [17,19,51–53]. Fat is the primary source of energy for migrating birds [21]; given the long journey in terms of distance, time and likelihood of encountering variable conditions, it follows that individuals with more fat are more likely to survive the crossing. The importance of day of the year was surprising and is probably owing to a combination of several factors leading to greater survival in early October compared with earlier and later in the season. Early October may be the optimal time to migrate because the amount of fruit available to thrushes and other migrants declines throughout autumn [54], while winds generally become more favourable later in the season. Taken together, these factors may define a narrow period in which individuals that leave in early- to mid-October optimize available food resources and the likelihood of encountering favourable winds. Although we accounted for fat, which would be related to fruit abundance and wind, it is possible that there are other aspects of bird health and environmental conditions that were not incorporated into our metrics. Alternatively, there may be other unmeasured intrinsic or extrinsic variables that happen to peak during this period.

This study attempts to quantify the risk small birds face when crossing a large geographical feature, but it is important to emphasize that apparent survival represents a minimal survival estimate. Some thrushes may have bypassed the YP and migrated through Veracruz or Cuba. However, Swainson's thrushes crossing to Veracruz would face an over-water flight of approximately 1500 km from FTM (1.5× greater than crossing to the Yucatan), which would probably reduce survival. Swainson's thrushes are also an uncommon migratory species in Cuba [55], which reduces the likelihood of bypassing the YP to the east. Although migrating across large bodies of water is often considered riskier than over land movement, our minimum estimates of survival for birds crossing the Gulf of Mexico under favourable conditions ($\varphi = 0.9$ with fat score greater than or equal to 4 and wind profit greater than 2) argue that this is not necessarily the case. As opposed to a barrier to migration, the Gulf of Mexico may represent a direct corridor for individuals with favourable departure conditions (i.e. high fuel loads and tail winds) to reach the wintering grounds quickly and safely, similar to what has been suggested for northern wheatears (*Oenanthe oenanthe*) crossing the Atlantic [56].

The decision to depart for the YP and the factors that influence whether an individual survives the journey may require individuals to hedge their bets. Swainson's thrushes are territorial on the wintering grounds [57], which may incentivize them towards early departure. The pressure to arrive on wintering grounds early represents an external force that presumably compels birds to select sub-optimal conditions to cross. Birds may optimize this time–risk trade-off by managing factors over which they exert some measure of control. The overall risk profile associated with crossing the Gulf may be mediated largely by fat acquisition, which makes food availability critical to managing the current risk landscape. For example, increasing fat stores beyond theoretical necessity [32] serves as a buffer that offsets risk posed by less than favourable winds and of course, carrying more fat can also be costly [58]. Our models show that a fat 3 thrush crossing with a 4 m s^{-1} wind profit experiences similar apparent survival as a fat 5 thrush crossing with a 2 m s^{-1} wind profit. By increasing their fat stores (a factor they can control), birds in effect increase the number of potential nights with favourable conditions, without excessively compromising risk. In addition, the early arrival on the breeding grounds may facilitate the acquisition of a high-quality wintering territory.

Among all phases of the avian annual cycle, previous studies have found the migratory period to be most limiting [59], and our analysis suggests that surviving a Gulf of Mexico crossing hinges on the availability of wind assistance and adequate fat stores. Climate change may affect wind profit [3], which varied widely within and among years during the study. Optimal wind profits in this study were identified as winds blowing towards the south and are generally associated with weather fronts [60]. Weather fronts out of the north (Nortes) produce strong south-directed winds favourable to birds crossing the Gulf. Pérez and colleagues [32] investigated how Nortes might change under projected climate change scenarios. They predicted an increase in the number of Nortes with strong winds favourable to migrating birds, albeit with shorter lifespans, lasting only a couple of days. Over the 25 years, we investigated change in favourable winds, which are probably associated with Nortes; we found an increase in frequency in favourable winds. However, it should be noted that the increase in the proportion of favourable nights (electronic supplementary material, figure S2) represents only about two more favourable nights across the 25 year period. This pattern, however, suggests a possible benefit of climate-induced changes in wind patterns for trans-Gulf crossing in autumn, albeit a more restricted window of favourability. If the duration of favourable weather systems shortens [32], birds will be pressed to deposit adequate fat stores and to make more judicious departure decisions.

Finally, our findings have clear conservation implications. Management of habitat that allows migratory birds to maintain or increase fat stores is needed. Migrants attempt to maximize fuelling opportunities during passage [61], but stopover habitats vary in quality [22,62]. Creation and protection of new stopover habitats, through restoration and land acquisition as well as management of existing habitats, should focus on vegetation types that increase the availability and diversity of food resources for migrating birds [63]. Our focal species, the Swainson's thrush, has declined throughout North America from 1966 to 2015 at an annual rate of 1.25% (95% CI −2.12 to −0.49) in the Eastern Region of the Breeding Bird Survey. This downward trend is reflective of many of the bird species migrating through our study area [64]. Clearly, thrushes and other species would benefit from conservation efforts directed towards stopover habitats, but protection of natural habitats is often at odds with urban development and other anthropogenic land-use changes common in coastal areas [65]. Although we focused on the Gulf of Mexico, long-distance migratory birds invariably encounter other large geographical features (e.g. oceans, deserts and mountain ranges) during passage and will probably rely on stopover areas where access to food resources and the ability to increase fat stores will create flexibility for minimizing risk in relation to negotiating these features.

Ethics. The capturing and banding of birds in Alabama was approved by the University of Southern Mississippi and the University of Illinois IACUC (no. 15154), the Bon Secour National Wildlife Refuge and conducted under the Federal Bird Banding Permit (21221).

Data accessibility. The capture history and weather data are archived at: https://databank.illinois.edu/; the capture history: https://doi.org/10.13012/B2IDB-2805211_V1; and the weather data: https://doi.org/10.13012/B2IDB-1311182_V1.

Authors' contributions. M.P.W. collected data and co-wrote the manuscript. T.J.B. conducted the mark-recapture analysis and co-wrote the manuscript. J.D. collected data and designed the research. T.J.Z. collected and analysed data. R.H.D. conducted the analysis of weather variables. A.C.-M. collected and analysed data. R.B. developed the weather model. F.R.M. established the long-term banding station and collected data. All authors contributed substantively to drafts of the manuscript.

Competing interests. We have no competing interests.

Funding. This work was supported by the National Science Foundation (NSF) (IOS awards 1146832, 1147096 and 1145952) and National Geographic Society's Committee on Research and Exploration (award 8971-11). T.J.Z. was supported by a NSF GK-12 Fellowship awarded to the University of Southern Mississippi (0947944), the Mississippi-Alabama Sea Grant Consortium (NA14OAR4170089) and the NOAA RESTORE Act Science Program (NA17NOS4510092).

Acknowledgements. We thank Jaclyn Smolinsky and the Fort Morgan banding station field technicians; M. Tabasco and W. Santamaria for assistance in the Yucatan Peninsula, L. Schofield, T. Beveroth, D. Enstrom, E. Swenson, W. Cochran and J. Cochran for assistance with telemetry aspects of the project; the USM radio tower crews and members of the USM Migratory Bird Research Group for their help and support. We also thank our numerous site partners in Alabama and the northern Yucatan Peninsula (Sisal, Yucatan to Isla Contoy, Quintana Roo) for assistance and permission to use their properties. Paul Cross provided valuable comments on the manuscript. Sarah Davidson and Gil Bohrer assisted us with obtaining NARR weather data from Movebank.org. Any use of trade, firm or product names is for descriptive purposes only and does not imply endorsement by the US Government.

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