

Original Article

What to do when stopping over: behavioral decisions of a migrating songbird during stopover are dictated by initial change in their body condition and mediated by key environmental conditions

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The behavioral decisions of migratory songbirds during migration stopovers can markedly influence the pace, efficiency, and success of migration. An individual's fuel stores are considered in theory to directly dictate subsequent stopover behavior (e.g., extent of foraging or vigilance, when to depart), although such decisions at stopover must also consider atmospheric factors (e.g., wind, precipitation) that influence the energetic costs of migration. We conducted the first study to date that directly manipulated the fuel stores of newly arrived songbirds at a stopover site, evaluated their effect on movement behavior and departure decisions, and assessed how atmospheric factors mediated these behavioral decisions. Hermit thrushes (*Catharus guttatus*) captured during fall migration at a southern New England, USA, offshore island stopover site and subsequently released with increased fuel stores moved less and made more tortuous movements, were more likely to depart on a given night and regularly resumed migration earlier and in a seasonally appropriate direction relative to individuals released with little change in fuel stores. The importance of fuel stores in modifying behavioral decisions increased throughout the migration period, presumably in response to declining food abundance. Precipitation suppressed migrant movements during stopover and precluded departure. Migrants departed in light winds with little respect to wind direction. The pervasive influence of fuel stores on migrant stopover behavior underscores the central role of fuel acquisition in the dynamics, speed, and success of migration, as well as the importance of quality stopover sites to migratory birds.

Key words: body condition, ecological barrier, fat, migration, songbirds, stopover.

INTRODUCTION

Billions of songbirds migrate to chase seasonally productive or escape seasonally deficient environments, moving over hundreds to thousands of kilometers as they traverse our rotating world (e.g., Alerstam 1990). Only in exceptional cases do migrants complete the journey in a single flight; most make multiple stopovers during which they rest and refuel for subsequent migratory flights. Typically, these migratory flights terminate at unfamiliar sites of variable quality, and it is there that migrants must secure the extraordinary amount of energy required for migration while balancing costs associated with predation, competition, and inclement

weather (Moore et al. 1995; Moore and Aborn 2000). Rebuilding this energetic capital results in roughly twice the time and energy expenditure during stopover than in migratory flight (Fransson 1995; Wikelski et al. 2003; Bowlin et al. 2005; Schmaljohann et al. 2012). This disproportionate allocation of time and energy to stopover, within the inherently challenging context of migration (e.g., Ketterson and Nolan 1982; Sillett and Holmes 2002; Menu et al. 2005; Strandberg et al. 2010; McKim-Louder et al. 2013), underscores the importance of stopover sites to migratory birds and suggests important fitness consequences follow from the choices made by migrants during stopover.

The behavioral decisions of migrants during stopover (e.g., movement dynamics and departure decisions) can markedly influence the pace, efficiency, and success of migration and result, in theory,

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from trade-offs among competing priorities of an overall migration strategy (i.e., maximizing migration speed, energy conservation, and safety; Alerstam and Lindström 1990; Houston 1998; Weber et al. 1998). The typical time constraint on migration (Hedenström 2008; Alerstam 2011) favors migrants that satisfy their energetic requirements efficiently, but resource acquisition and the subsequent transport of accumulated fuel entail energetic and exposure costs (e.g., Metcalfe and Furness 1984; Klaassen and Lindström 1996; Kullberg et al. 1996; Lind et al. 1999). Consequently, at any time, an individual's fuel stores may determine its behavioral priorities (e.g., foraging or vigilance) and thus dictate subsequent stopover behavior and departure decisions. For example, tracking individual migrants across a spectrum of natural body conditions suggests that migrants with depleted fuel stores and thus increased energy demands alter their foraging and movement behavior, typically making faster, longer, and more linear (less area-restricted) movements during stopover (Loria and Moore 1990; Moore and Aborn 2000; Wang and Moore 2005; Tietz and Johnson 2007; Ktitorov et al. 2010; Matthews and Rodewald 2010a; Seewagen et al. 2010; Cohen et al. 2012; but see Chernetsov and Muhkin 2006; Paxton et al. 2008; Seewagen et al. 2010; Arizaga et al. 2013). Additionally, migrants in better energetic condition more regularly depart stopover sites in a seasonally appropriate direction (reviewed in Sandberg 2003; see also Deutschlander and Muheim 2009; Covino and Holberton 2011; Schmaljohann et al. 2011; Schmaljohann and Naef-Daenzer 2011; Smolinsky et al. 2013). The association between fuel stores and the duration of stopover is less consistent although migrants with larger fuel stores regularly spend less time at a given stopover site (Biebach 1985; Dierschke and Delingat 2001; Schaub et al. 2008; Goymann et al. 2010; Matthews and Rodewald 2010b; Seewagen and Guglielmo 2010; Morganti et al. 2011; Andueza et al. 2013; Bulyuk and Tsvey 2013; Smolinsky et al. 2013; Cohen et al. 2014; but see Dierschke and Delingat 2001; Chernetsov and Muhkin 2006; Bolshakov et al. 2007; Salewski and Schaub 2007; Tsvey et al. 2007; Ktitorov et al. 2010; Seewagen et al. 2010; Andueza et al. 2013). Studies supplementing free-ranging migrants with food during stopover (summarized in Schmaljohann et al. 2013) have proved useful in evaluating the influence of body condition on these departure decisions. Despite this body of evidence, no previous study has directly manipulated migrant body condition and explored the consequences of this manipulation on subsequent stopover movement and departure dynamics.

The stopover dynamics of individual migrants vary also with environmental conditions. Atmospheric conditions, wind and precipitation in particular, profoundly influence the timing, intensity, energetics, and geography of avian migration (Richardson 1978; Alerstam 1990; Richardson 1990). During fall migration in the northern hemisphere, for example, many birds migrate preferentially in the days following cold fronts when winds typically provide some tailwind assistance (Able 1973; Richardson 1978, 1990; but see Karlsson et al. 2011). This benefit is likewise expected to influence individual decisions to resume migration (Liechti and Bruderer 1998; Weber and Hedenström 2000) although empirical work is more equivocal (e.g., Fransson 1998; Åkesson and Hedenström 2000; Schmaljohann et al. 2011; Smolinsky et al. 2013). Nonetheless, these otherwise favorable conditions can concentrate migrants along topographic barriers (Åkesson 1993; Hüppop et al. 2006; Gagnon et al. 2011), where the importance of fuel stores and atmospheric conditions on stopover decisions may be more profound (Jenni and Schaub 2003; Tsvey et al. 2007; Schaub et al. 2008).

We explored the dynamics of songbird stopover in relation to fuel stores, atmospheric conditions, and resource availability in the context of naive migrants displaced to an offshore island in southern New England, USA (Block Island, RI). We experimentally manipulated the fuel stores of newly arrived birds and tracked their subsequent movements and departure decisions via radio telemetry. Relative to mark-recapture data and their associated probability models (e.g., Salewski and Schaub 2007; Schaub et al. 2008; Arizaga et al. 2011), telemetry dramatically improves certainty in estimates of stopover duration (Tsvey et al. 2007; Seewagen and Guglielmo 2010) and, moreover, enables the estimation of movement dynamics during stopover. We tested the following hypotheses related to the condition dependence of behavioral decisions made by migrating songbirds at stopover sites: birds released with larger fuel stores experience reduced energy demand and thus 1) move less and make less directed, more tortuous movements during stopover. However, these condition-dependent movement differences vary with context: fuel stores at release may be most relevant 2) in the first day(s) after release and 3) later in the fall due to increased time constraints and declining food resources. Fuel stores also dictate departure decisions—birds with larger fuel stores 4) are more likely to depart than leaner birds on any given night and resume migration sooner and 5) depart more regularly in a seasonally appropriate direction. We also tested the following hypotheses related to how atmospheric conditions mediate the movement and departure decisions of migrating songbirds at stopover sites: 6) precipitation generally inhibits diurnal movements and departure of individuals, and 7) wind speed and direction influence an individual's decision to depart as well as the direction of departure. The simultaneous release of individual migrants with manipulated fuel stores and their subsequent tracking controlled for important confounding variables at the time of release (e.g., resource abundance, predation risk, weather, and endogenous time program) and so provides the most direct test to date of these hypotheses regarding the condition dependence of behavioral decisions of migrating songbirds.

METHODS

Study area

The field experiment occurred during the autumnal migrations of 2009 and 2010 on Block Island (41°28'N, 71°31'W), a 25-km² glacially deposited landmass located approximately 15 km south of the Rhode Island mainland and 23 km east-northeast of Long Island, NY (Figure 1). During fall migration, westerly winds associated with passing cold fronts displace large numbers of migratory songbirds, particularly hatching year birds, to the coast and offshore islands such as Block Island (e.g., Baird and Nisbet 1960; Able 1977). Once on Block Island, migrating songbirds rest and refuel extensively in the maritime shrub community, consuming large quantities of fruit in the process (Parrish 1997; Smith et al. 2007; Bolser et al. 2013). The species composition and structure of the maritime shrub community is dictated largely by exposure to salt spray and wind (Enser and Lundgren 2006). Highly exposed areas near the coast are dominated by short-statured bayberry (*Morella pennsylvanica*), poison ivy (*Toxicodendron radicans*), and roses (*Rosa* sp.), brambles (*Rubus* sp.), and briars (*Smilax* sp.). More protected areas are dominated by native shadbush (*Amelanchier canadensis*), arrowwood (*Viburnum recognitum* and *Viburnum dentatum*), chokeberry (*Aronia prunifolia*, *Aronia melanocarpa*, and *Aronia arbutifolia*), winterberry (*Ilex verticillata* and *Ilex laevigata*), bayberry, and Virginia creeper (*Parthenocissus quinquefolia*), as well as the invasive multiflora rose (*Rosa multiflora*) and Oriental

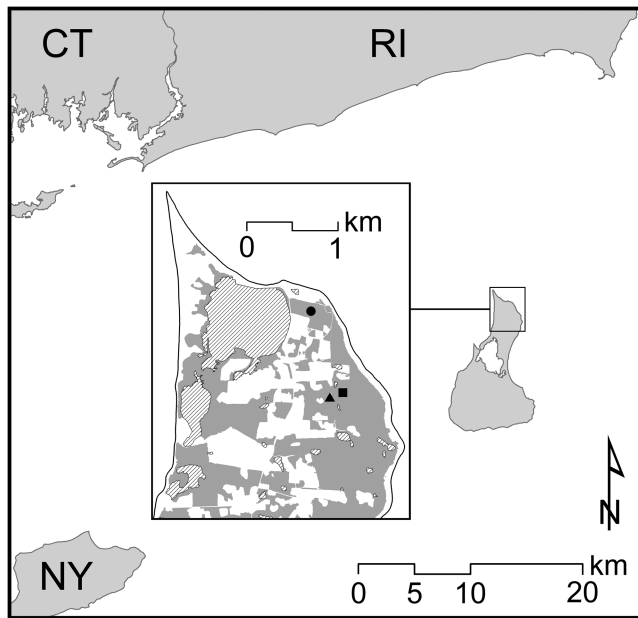


Figure 1

Geographical context of Block Island, Rhode Island (RI), USA, where we experimentally investigated the role of fuel stores on stopover movements and departure decisions in Hermit thrushes during the fall migrations of 2009 and 2010. Thrushes continued migration toward Long Island, New York (NY) or returned to mainland Rhode Island or Connecticut (CT); both options involved flights of about 20–30 km. (Inset) We captured thrushes (filled circle) at the northern extreme of the maritime shrub community (shaded areas). After capture, thrushes were placed in temporary captivity (filled triangle) for 2–6 days, after which they were released in contiguous maritime shrub habitat from a soft release aviary (filled square). Bodies of water are indicated by cross-hatching.

bittersweet (*Celastrus orbiculatus*). Pokeweed (*Phytolacca americana*), a large berry-producing perennial herbaceous plant, is also locally common throughout the maritime shrub community.

Bird capture

We used mist nets to capture Hermit thrushes (*Catharus guttatus*) at the northern extent of the maritime shrub community on Block Island, a location where recently arrived songbirds congregate (e.g., Baird and Nisbet 1960; Able 1977; Figure 1, filled circle). Hermit thrushes (hereafter thrushes) are common temperate migrants that use the fruits of the maritime shrub community extensively during stopover on Block Island (Parrish 1997; Smith and McWilliams 2010). We captured thrushes for this field experiment in a way that maximized the likelihood that individuals were new arrivals to Block Island with limited prior experience with the distribution or quality of resources. First, we used only hatch-year thrushes captured on mornings (1 h before to 1 h after local sunrise) following nights favorable for the arrival of migratory birds to Block Island (i.e., westerly or northerly winds in the day[s] following cold front passage). Second, we broadcasted thrush flight calls (Evans and O'Brien 2002) throughout the night until 1 h before sunrise, at which time we switched to mixed thrush songs and calls (Elliott et al. 2010); previous work suggests that newly arrived birds are likely more influenced (and attracted) by broadcasted calls than settled migrants (Schaub et al. 1999; Fransson et al. 2008). Thrushes possessed reduced fat and breast muscle scores at capture (see Results), which further supports our assumption that these individuals were recent arrivals.

Field captivity and fuel stores manipulation

After capture, we measured wing chord (± 0.5 mm) and body weight (± 0.1 g) and assessed visible subcutaneous fat on an 8-point scale (DeSante et al. 2003) and breast musculature on 4-point scale (Bairlein 1995); we regularly assigned both measures in half-score increments. On a given morning, we transported up to 12 hatching year birds less than 1 km from the capture site and placed them in a holding aviary for the manipulation of fuel stores (Figure 1, filled triangle). We housed birds individually in stainless steel cages (36 cm \times 43 cm \times 60 cm) in an enclosed permanent structure that protected thrushes from the elements but nonetheless exposed them to natural photoperiod and temperature fluctuations. We paired birds with similar initial size and condition metrics (cf. Morris 1996) and then assigned 1 thrush of each pair randomly into 1 of 2 feeding regimes: 1) a “maintenance” group provided 8–9 g (wet) of live wax moth larvae (waxworms; *Pyralidae*) each day and 2) an “ad libitum” group provided more waxworms than could be consumed each day (up to 20 g); we provided all thrushes with water ad libitum. We monitored food consumption and body mass daily. Field captivity typically lasted 3–4 days (80% of thrushes) although some thrushes remained in captivity from 2 to 6 days (the latter due to inclement weather conditions).

Transmitter attachment, release, and tracking

We fitted thrushes with a 0.77 g (maintenance) or 1.00 g (ad libitum) radio transmitter (Holohil® BD-2) less than an hour prior to placement into a release aviary (see below). We glued (Torbot ostomy bonding cement; Cranston, RI) the transmitter between the shoulders after trimming a small patch of feathers nearly to the skin. We used transmitters of different mass to impose a similar relative mass burden on thrushes in different treatments at release; transmitters represented on average $2.8 \pm 0.2\%$ of the release weight of thrushes. We expected negligible differences in behavior due to, for example, a decreasing relative burden as maintenance thrushes gained weight during stopover (Schmidt-Wellenburg et al. 2008). Capture, handling, and transmitter attachment activities were approved by our Institutional Animal Care and Use Committee (A98-09-012).

We typically released thrushes in cohorts of 4 thrushes (i.e., 2 pairs; range 2–10 thrushes) comprising equal numbers of birds from each diet treatment with identical capture, captivity, and release histories. To standardize releases among individuals, we located a release aviary in contiguous maritime shrub habitat (Figure 1, filled square). We constructed the release aviary by surrounding a mature bayberry shrub with a wooden frame (2.5 m tall \times 1.5 m wide \times 1.5 m long); we fabricated the sides and ceiling from heavy canvas. We left the bottom 1 m of the enclosure open to the environment and provided numerous perches (in the form of downed limbs, brush, etc.) around the base of the aviary to encourage a controlled exit from the aviary. We placed thrushes by hand into the enclosed bayberry shrub in total darkness within a few hours of sunset. Thrushes never attempted escape during the night and exited the enclosure via the unenclosed bottom the subsequent morning. Our observations of exiting thrushes suggest that this release method eliminated the occurrence of “agitation dispersal,” an increase in movement and activity associated with release after captivity and marking (Buler 2006).

After thrushes exited the aviary (morning of day 1), we recorded their locations throughout the day (from morning to evening civil twilight) for up to 4 days of stopover ($n = 29$). If individuals stayed on island longer than 4 days ($n = 21$), we checked their status (i.e.,

location and health) daily until they departed. Our protocol for locating individuals throughout the day varied between the 2 years of the study. In 2009, 3 observers triangulated the location of each thrush ($n = 18$) every 45 min (median; interquartile range [IQR]: 21–75 min). In 2010, observers tracked and estimated the location of individual thrushes ($n = 32$) every 11 min (IQR: 9–14 min). We recorded the bearing and estimated distance to thrushes (<50 m) from points georeferenced with a handheld Global Positioning System and used trigonometry to derive the location estimates. Prior to tracking each year, we tested observers' ability to locate transmitters hidden throughout the maritime shrub community; tests suggested that the 2 methods provided thrush locations accurate to approximately 19 m (median; IQR: 14–31 m) and 8 m (median; IQR: 4–10 m), respectively.

We also monitored at-large thrushes every 1–4 h throughout the night to determine the timing and direction of their departure from Block Island. We tracked departing thrushes over the open ocean from a slightly elevated (3–10 m above sea level) position near the shoreline. We recorded departure direction as the bearing at which the signal was lost. We estimated the signal range over the ocean at ~6 km by holding a transmitter in a position similar to a flying thrush atop a ferry leaving Block Island. We typically maintained contact with thrushes departing Block Island over open water for well over 10 min, which suggests, assuming some wind assistance and an air speed of 10 m/s (Cochran and Kjos 1985), that our 6 km estimate represented a minimum detection range during departure. On days subsequent to a recorded departure, we checked for the presence of each individual to ensure that they had left the island rather than returned and relocated.

Abundance of arthropods and fruits during fall migration

From 16 September to 12 November 2010, we monitored seasonal patterns of abundance in fruiting plants and ground-dwelling arthropods in about 12-ha study area around the release aviary. We assessed resource abundance around the release aviary because the location where migrants "land" is likely to be critical in determining the resources ultimately available at a stopover (Paxton et al. 2008). We monitored arthropod abundance with pitfall traps at 17 sites, randomly located within 3 habitat strata: small (<0.1 ha) mixed annual and perennial grasses and herbs ($n = 5$), upland maritime shrub ($n = 6$), and wetland maritime shrub (within 10 m of permanent water, usually a kettle pond; $n = 6$). Pitfall traps consisted of large tin cans (15.3 cm diameter) buried such that the rim was slightly below soil (not leaf litter) level and surrounded with 3 drift fences (0.6 m lengths of aluminum flashing) spaced at approximately 120° around the rim's circumference. We placed a circular resin-coated (Tanglefoot; Contech Enterprises, Victoria, British Columbia) board in the bottom of each can to trap arthropods falling into the can and facilitate the counting of individual arthropods. To operate, we installed the resin-coated inserts for a period of 8–9 h beginning within 1 h of sunrise, after which we counted the arthropods, removed and cleaned the inserts, and raised the top of the can above ground level. We operated pitfall traps approximately weekly throughout the study period ($n = 8$ sampling occasions) on days with no precipitation and light to moderate winds.

We monitored the abundance of fruits on 6 plant species consumed regularly by migrant songbirds on Block Island (northern arrowwood, Virginia creeper, pokeweed, bayberry, winterberry, and multiflora rose; Parrish 1997; Smith et al. 2007; Bolser et al. 2013). We located the nearest healthy, fruiting individual of each species

within 15 m of 8 random sites within the study area. We continued to add random sites until each species was represented by 6–8 individual plants. On each individual, we counted fruits on 1–3 representative marked branches approximately weekly throughout the study period ($n = 8$ sampling occasions).

Atmospheric conditions

We gathered weather data from the Block Island State Airport, which reported conditions every 15 min (National Climatic Data Center QCLCD 2.5.4; <http://cdo.ncdc.noaa.gov/qclcd/QCLCD?prior=N>, accessed 28 July 2013). We first calculated wind profit from wind direction and wind speed (Erni et al. 2002); wind profit represents the distance a bird is drifted toward a migratory goal in a fixed time interval through only the effect of wind. Wind profit calculations require the user to specify the direction of this migratory goal. We calculated 2 versions of wind profit to capture the 2 primary migratory goals for thrushes leaving Block Island: 1) an "onward migration" wind profit with the nearest land point of Long Island, NY, as the migratory target (240°) and 2) a "reverse migration" wind profit with the nearest point of the Rhode Island mainland as the migratory target (345°). We propose that these definitions adequately captured those combinations of wind direction and speed that facilitate "onward" or "reverse" migration, respectively. We calculated nightly averages of wind profit variables from 35 to 39 observations throughout a given night (evening civil twilight to the subsequent morning civil twilight). We also calculated the proportion of hours during a given night or day (morning civil twilight to evening civil twilight) that the weather station reported any measurable precipitation.

Statistical analysis

Our experimental manipulation dichotomized feeding regime (maintenance vs. ad libitum) among individuals. However, variation in the quantity of waxworms consumed resulted in informative variation in the magnitude of condition changes among birds, particularly those in the ad libitum regime. We thus evaluated the influence of the change in fuel stores during captivity rather than the dichotomized feeding regime because it more precisely captured the effect of our dietary manipulation. We constructed a generalized additive mixed model (GAMMs; Wood 2006) for thrush body mass using wing chord, subcutaneous fat score, and breast musculature score from which we estimated the fat free mass (hereafter, lean mass) and fat mass (the difference of lean mass from total mass) of each thrush at capture and release. From these estimates, we derived changes in lean and fat mass during captivity. Because the change in thrush body mass during captivity was due predominantly to changes in fat mass (see Results) and fat is the primary fuel of migration (Blem 1990; McWilliams et al. 2004), we used the estimated fat mass at release as our measure of thrush fuel stores in all subsequent analyses.

Our pairing of birds with similar body size, condition scores, and thus estimated fuel stores at capture (ad libitum thrushes with 0.2 ± 1.1 g [mean \pm standard deviation (SD)] reduced initial fuel stores; statistically equivalent to within ca. 0.5 g based on a paired t -test of equivalence; Wellek 2003) guaranteed a strong correlation between fuel stores at release and the change in fuel stores during captivity ($r = 0.94$, $t_{24} = 19.7$, $P < 0.001$; within-pair correlation sensu Bland and Altman 1995). We were thus unable to distinguish the effects of change in fuel store from current fuel store (i.e., at release). However, we think it more likely that current fuel store

(i.e., at release) is the more important metric and justifies its use. We note that substituting the change in fuel stores during captivity for fuel stores at release produced nearly identical quantitative and qualitative results.

We quantified multiple aspects of thrush movement. We evaluated the quantity of daily movement (i.e., the cumulative summed distance between estimated locations; total distance) and the straight-line distance from the initial morning location to the final (typically roosting) location (i.e., linear displacement). An index of area-restricted movement is often calculated as the quotient of linear displacement and total distance moved (e.g., Williamson and Gray 1975; Paxton et al. 2008). However, linear displacement and this index were highly correlated in thrushes ($r = 0.77$, $t_{49} = 17.0$, $P = 0.002$; within-subject correlation), so we used only linear displacement in all our analyses.

We modeled total movement and linear displacement as functions of thrush fat mass at release, the time since release (i.e., day of stopover, up to 4 days), ordinal date (i.e., seasonal effects), and the proportion of the day with reported precipitation. We also fitted the 2-way interactions between fat mass and both stopover day and seasonal effects. We estimated these associations in linear mixed effect models (LMMs) that included a random effect for thrush pairs within cohorts and a random intercept and slope (over stopover day) for each thrush (Schielzeth and Forstmeier 2009). In our evaluation of total distance moved each day, we included an offset term for the time (h) an individual was tracked each day (typically all day, although day length shortened as the season progressed) as well as the number of daily estimated locations and tracking method as covariates. We applied a log transformation to both response variables to stabilize residual variances.

We modeled the nightly decision to depart (i.e., the hazard of departure) as a function of fat mass at release and its interaction with the current length of stopover, ordinal date, and the nightly average values of wind profit for onward and reverse migration using a mixed effects Cox regression model (Cox 1972; Therneau 2000). Current stopover length, wind profit variables, and ordinal date were time-varying covariates (changing nightly). We did not consider the proportion of the night with reported precipitation because only 1 of the 44 thrushes with known departures left on a night with measurable precipitation (and it left prior to the occurrence of precipitation); this observation dictated the parameter estimate for the precipitation effect and, furthermore, its removal made the parameter inestimable. The stopover record for 6 thrushes (see below) was right censored (i.e., did not record a departure event). We included random effects (Gaussian frailty terms; Therneau 2000) for thrush pairs within cohorts.

We evaluated stopover duration (days) as a function of fat mass at release, ordinal date of release, and their interaction using a generalized (Poisson) LMM. We included a random intercept for thrush pairs within cohorts. We excluded from this analysis 6 thrushes (5 maintenance and 1 ad libitum) without recorded departures. Four thrushes failed to depart prior to the end of field work, 1 thrush lost its transmitter after 4 days (with no indication of depredation or fatality), and 1 thrush sustained an injury on its seventh stopover day.

We further explored departure decisions among 25 thrushes with known departure times and directions. We dichotomized these departures into 2 categories: “onward” migration toward Long Island (departure directions between 219° and 270°) and “reverse” migration toward the Rhode Island mainland (departure directions between 287° and 10°). The small sample size (i.e., 13 onward

migration “events”) greatly restricted the analysis; we thus constructed a mixed effects logistic model that included only fat mass at release and random effects for thrush pairs within cohorts and we cautiously interpreted these model results. We evaluated how time of departure (proportion of night elapsed) varied with fat mass at release, stopover duration, or the departure direction (i.e., onward or reverse) using a LMM that included random effects for thrush pairs within cohorts and the night of departure (to account for environmental conditions).

We conducted all analyses in R 3.0.1 (R Core Team 2013). We implemented GAMMs using the *gamm4* package (Wood and Scheipl 2013). We compared the change in fat mass among paired thrushes attributable to dietary manipulation using a paired *t*-test. We evaluated LMMs and generalized (Poisson and logistic) LMMs using the *lme4* package (Bates et al. 2013). We estimated the mixed effects Cox model using the *coxme* package (Therneau 2012); we evaluated fixed effects with likelihood ratio tests. Residuals in several linear analyses were somewhat heavy tailed at one end of the distribution, so we compared parameter estimates and their associated variation with the corresponding estimates from 1000 nonparametric bootstraps of the model fit (Ren et al. 2010). Estimates compared favorably between the 2 methods, so we based estimates, confidence intervals (CIs), and associated figures on the maximum likelihood estimates (or adaptive Gauss–Hermite quadrature approximations in the logistic model), although we report the significance of parameters based on comparisons with 1000 parametric bootstraps of a reduced model excluding the parameter. Finally, we evaluated the importance of covariate interactions with fat mass based primarily on plots of the marginal effects of fat mass on the response variable (and their associated uncertainty) across the range of values of the covariates, as assessing interactions using only the significance test risks missing important conditional relationships (Brambor et al. 2006).

RESULTS

Manipulation of thrush fuel stores

Thrushes assigned to different diet regimes initially possessed similar subcutaneous fat and breast musculature scores (Figure 2A). Maintenance birds retained similar condition scores during captivity, whereas ad libitum birds significantly increased their fat scores and, to a lesser extent, breast musculature scores (Figure 2A). The body mass of ad libitum thrushes increased at a rate of 1.6 g per day (± 0.6 SD; range: 0.8–2.9 g per day), whereas the mass of maintenance birds remained stable while in captivity ($0.1 \text{ g} \pm 0.3 \text{ SD}$; range: -0.5 to 0.6 g per day; Figure 2B). The rate of mass gain in ad libitum thrushes was similar to the maximum rate of mass gain observed in nonexperimental thrushes recaptured in the study area (1.7 g per day; Smith A, unpublished data). Wing chord, fat score, and breast muscle score related strongly and positively to thrush body mass and together explained about 61% of the variation in body mass although the form of the relationship varied among the 3 measurements (Figure 3). Changes in thrush mass during captivity were due largely to gains in fat (Figure 2B), which typically comprised more than 90% (median; IQR: 69–100%) of the total change in body weight. Diet regime affected the change in fat mass in ad libitum thrushes during captivity ($t_{24} = 12.0$, $P < 0.001$; Figure 2B), which gained 4.5 g (median; IQR: 3.5–5.4 g) of fat during captivity; maintenance thrushes gained little fat during captivity (median: 0.0 g; IQR: -0.1 to 0.6 g). Subsequent to the dietary manipulation, maintenance and ad libitum thrushes were released with 1.9 g (median; IQR: 1.0–3.0 g) and 6.3 g (median; IQR:

5.2–7.6 g) of fuel stores, respectively. Fat mass at release correlated strongly with fuel load (i.e., estimated fat mass divided by estimated lean mass; $r = 1.00$, $t_{48} = 118.92$, $P < 0.001$) and fuel deposition

rate during captivity (Δ fuel load per day; $r = 0.78$, $t_{48} = 8.58$, $P < 0.001$).

Thrush movements

Fuel stores affected the aggregate of daily movements in migrating thrushes, but the effect varied seasonally (fat \times season interaction; parametric bootstrap $P[P_{pb}] = 0.05$). Fuel stores exerted little influence on thrush movements early in migration (Figure 4A). However, thrushes decreased their total daily movement by on average about 11% per gram of fuel stores late in the migratory period, corresponding to about 60% more total daily movement for a thrush with a 2-g fat mass (a typical maintenance thrush) relative to a thrush with 6-g fat mass (a typical ad libitum thrush; Figure 4C). Thrushes released with more substantial fuel stores exhibited a consistent pattern of movement during stopover throughout the migratory season, whereas leaner thrushes exhibited a considerable seasonal increase in their daily movements, particularly in the first day(s) of stopover (Figure 4). All thrushes reduced their total daily movement approximately 14% per day (95% CI: 8–19%; $P_{pb} = 0.002$) as stopover progressed, and the effect varied little with fuel stores (Figure 4; fat \times stopover day interaction; $P_{pb} = 0.26$). We also found evidence that every 10% increase in the proportion of the day with reported precipitation associated with an additional 8% (CI: 3–12%; $P_{pb} = 0.009$) reduction in total daily movement.

The fuel stores of thrushes at release likewise influenced the extent of their linear, presumably exploratory, movements. However, this influence applied primarily to leaner thrushes and varied with stopover and seasonal contexts. Lean thrushes quickly restricted the directedness of their movements as stopover progressed, whereas thrushes released with more substantial fuel stores exhibited consistent patterns of linear displacement with little regard to stopover context (fat \times stopover day interaction; $P_{pb} = 0.05$; Figure 5). For example, a thrush released with a 2-g fat mass reduced its linear displacement roughly 26% with each successive stopover day compared with an approximately 6% daily reduction in a thrush with a 6-g fat mass at release (Figure 5). Furthermore, leaner thrushes used increasingly linear movements as migration progressed. Late in migration, the typical maintenance thrush (i.e., 2-g fat mass) ranged about twice as far on its first day of stopover as a similar thrush early in migration (cf. solid lines in Figure 5A,C); daily displacement movements of thrushes carrying more substantial fuel stores remained consistent throughout the migration period (Figure 5).

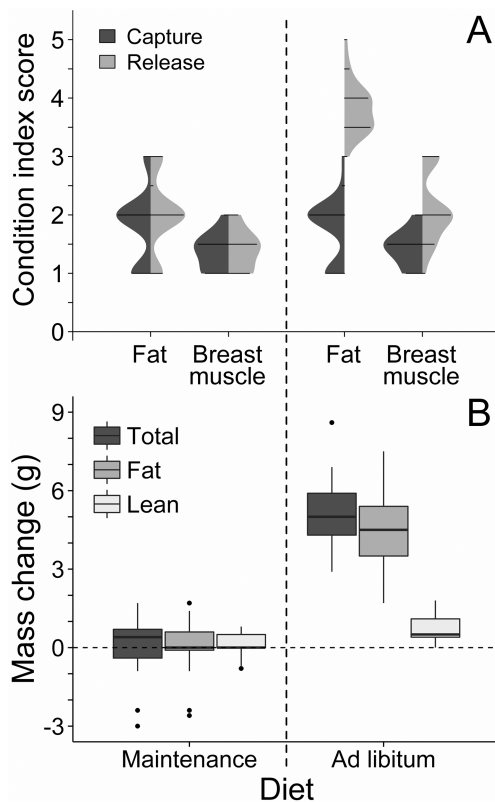


Figure 2

Hermit thrush fuel stores were modified by feeding regime (maintenance vs. ad libitum) provided to short-term captive birds over on average 3–4 days during the fall migrations of 2009 and 2010 on Block Island, RI, USA. (A) Bean plots illustrating the distribution of subcutaneous fat and breast musculature indices scores for maintenance and ad libitum thrushes at capture and release. Horizontal lines within the bean plots indicate the relative number of individuals with a given condition score ($n = 25$ in each feeding regime). (B) Changes in body composition of maintenance and ad libitum thrushes during captivity. See text for details of diet treatment and body composition estimation.

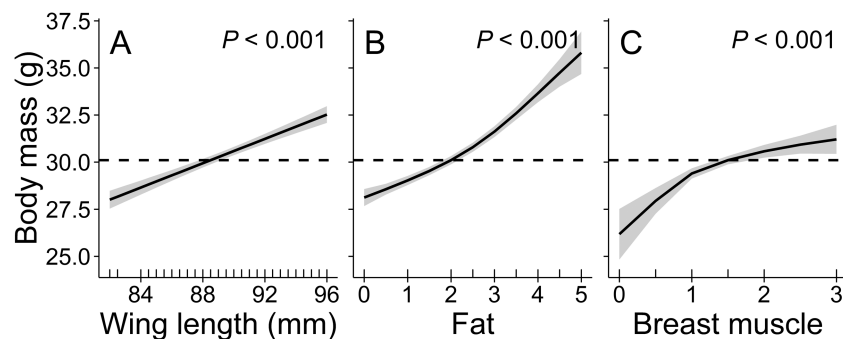
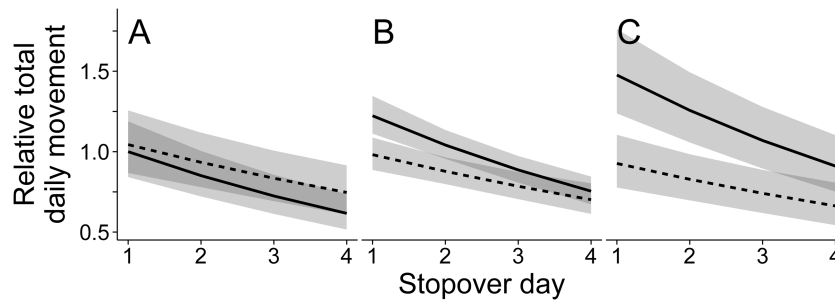
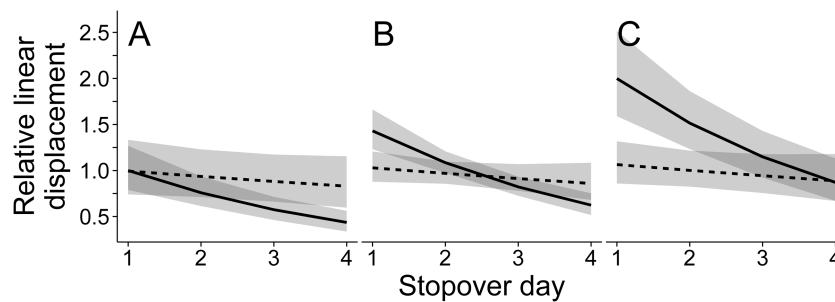


Figure 3

Relationships between body mass and (A) wing chord, (B) subcutaneous fat score, and (C) breast musculature score from 484 observations on 294 Hermit thrushes captured on Block Island, RI, USA during the fall migrations of 2009 and 2010. The solid line indicates the relationship (penalized spline) between a variable and body mass while other variables are held at their medians; shaded areas around this line indicate the 95% CI for the relationship. The dashed horizontal line indicates the predicted body mass when all measures are at their medians. The rug plot along the abscissa indicates observed values of a given variable. The model explained ~61% of the variation in thrush body mass.

**Figure 4**

Total daily movements of Hermit thrushes with reduced body fat (2-g fat mass; solid line) and substantial body fat (6-g fat mass; dashed line) on Block Island, RI, USA, during (A) early, (B) middle, and (C) late thrush migration in autumn 2009 and 2010. Movements are scaled relative to a thrush with reduced body fat early in the season on its first day of stopover (i.e., after release) to facilitate comparisons. Lines and shading indicate the fitted conditional relationships and their associated standard error, respectively. Sampling effort was roughly equal during each third of the migration season ($n = 14, 16,$ and 20 , respectively, for the first, middle, and last third).

**Figure 5**

Daily linear displacement of Hermit thrushes with reduced body fat (2-g fat mass; solid line) and substantial body fat (6-g fat mass; dashed line) on Block Island, RI, USA, during (A) early, (B) middle, and (C) late thrush migration in autumn 2009 and 2010. Linear displacement was scaled relative to a thrush with reduced body fat early in the season on its first day of stopover (i.e., after release) to facilitate comparisons. Lines and shading indicate the fitted conditional relationships and their associated standard error, respectively. Sampling effort was roughly equal during each third of the migration season ($n = 14, 16,$ and 20 , respectively, for the first, middle, and last third).

The consequence of these conditional relationships on the use of linear movements is straightforward—thrushes exhibit relatively similar ranging behavior early in migration, with little regard to fuel stores, whereas later in migration, lean thrushes become increasingly more mobile than fatter thrushes albeit primarily in the first day(s) of stopover. Increased precipitation reduced linear displacement as it did total movement; every 10% increase in the proportion of the day with reported precipitation was associated with an additional 16% (CI: 7–24%; $P_{pb} = 0.003$) reduction in linear displacement.

Thrush departure decisions and stopover duration

Thrushes departed Block Island 1–13 days (median: 4 days) following their release. Sixteen thrushes (12 ad libitum and 4 maintenance) left after the first day of stopover. Fat mass influenced the length of thrush stopover more generally as well. Stopover duration decreased approximately 10% per gram of fat (CI: 3–16% per gram; $P_{pb} = 0.004$), a relationship that remained consistent throughout migration (fat \times season interaction; $P_{pb} = 0.73$). Thus, a thrush with a 6-g fat mass at release was estimated to stay approximately 3 days compared with 4–5 days for a thrush with a 2-g fat mass released at the same time or roughly a 50% increase in stopover duration for the leaner thrush. Thrush stopover duration did not change appreciably throughout the fall migration period ($P_{pb} = 0.70$).

Fat mass at release influenced nightly decisions to depart Block Island. The hazard for departure on the first night of stopover increased 24% per gram of fat (CI: 2–51% per gram; $\chi^2 = 6.91$, $P = 0.009$), suggesting more than a 2-fold higher hazard of departure for a thrush released with a 6-g fat mass relative to that of a thrush with a 2-g fat mass. This hazard did not effectively change as stopover progressed (fat \times stopover day interaction; $\chi^2 = 0.28$, degrees of freedom [df] = 1, $P = 0.59$). Thrushes departed under a variety of wind speeds although most left on nights with average wind speeds less than 5 m/s (median: 4.7 m/s; range: 1–9 m/s); indeed, departure hazard decreased 18% for every meter per second increase in wind speed (CI: 1–31% m/s; $\chi^2 = 4.66$, $P = 0.03$). Thrush departure hazard decreased in wind conditions favoring a reverse migration to the mainland ($\chi^2 = 1.87$, df = 1, $P = 0.17$) and increased in wind conditions favoring onward migration to the southwest ($\chi^2 = 2.26$, df = 1, $P = 0.13$), but not consistently. Only thrushes returning to the mainland departed into headwinds although the vanishing direction of most thrushes was profoundly influenced by wind direction during departure.

We documented the departure time and direction of 25 thrushes: 13 (52%) left Block Island to the west or southwest in apparent onward migration, whereas the other 12 (48%) departed to the northwest or north in apparent reverse migration. Fat mass at release influenced the decision to undertake onward versus reverse migration. Specifically, the odds of onward migration increased ~52% per gram of fat at release (CI: 1% decrease–133% per gram

increase), corresponding to 0.69 and 0.30 predicted probabilities of undertaking onward migration for thrushes released with 6 and 2 g of fat, respectively. Thrushes departed Block Island 1.3–5.7 h after sunset (median: 3.1 h). Time of departure varied with the departure direction with thrushes making onward migrations toward Long Island leaving 13% nearer to sunset (CI: 4–21%; $P_{pb} = 0.01$; IQR: 1.8–3.1 h) than those returning to the mainland (IQR: 3.0–5.1 h), but there was little evidence to suggest that the time of departure varied with thrush fat mass at release ($P_{pb} = 0.75$) or stopover length ($P_{pb} = 0.37$).

Patterns of resource abundance

Ground-dwelling arthropod abundance varied considerably throughout the fall migration (Figure 6A) but provided little indication of a consistent decline (or increase). In contrast, once fruits had ripened, fruit abundance declined throughout the fall for all species (Figure 6B). The decline was particularly steep for highly nutritious fruits commonly eaten by Hermit thrushes such as arrowwood and Virginia creeper (Figure 6B; AW and VC, respectively).

DISCUSSION

We experimentally manipulated songbird fuel stores during migration stopover and evaluated their subsequent influence on multiple aspects of movement behavior and departure decisions. We found that the influence of fuel stores (or possibly fuelling rate; see below) pervaded migrant stopover behavior including the amount and

directedness of daily movement, stopover duration, nightly decision to depart, and the direction of that departure. Nonetheless, the relationship between fuel stores at release and stopover behavior often varied within the context of stopover and season. Atmospheric conditions likewise influenced patterns of movement and departure decisions.

Manipulation of thrush fuel stores

Experimental manipulation of body mass produced predominately affected the stored fat mass of thrushes. Thus, we evaluated stopover behavior and departure decisions in the context of this absolute measure of fuel stores. However, migrants may base behavioral decisions during stopover on other intrinsic conditions rather than absolute fat stores. For example, given the important energetic contributions of protein during migration (Jenni and Jenni-Eiermann 1998; Bauchinger and Biebach 2001), migrants may also monitor changes in lean mass, which suggests that a composite measure of condition that accounts for changes in protein or muscle mass during stopover (e.g., Fusani et al. 2009; Seewagen and Guglielmo 2010; McWilliams and Whitman 2013) may be relevant. Alternatively, migrants may base decisions on relative changes in condition such as the rate of fuel accumulation (i.e., fuel deposition rate; Morris 1996; Hedenström and Ålerstam 1998; Schaub and Jenni 2000; Eikenaar and Schläpke 2013) or the rate of fuel loss prior to stopover (Eikenaar and Bairlein 2014), though the latter is practically impossible to measure. We were unable to evaluate the potential importance of these different measures of individual fuelling state due to minimal changes in estimated lean mass and strong correlations between fuel deposition rate and mass change during captivity and estimated fat mass at release.

Condition dependence of thrush movement

When we detected condition-dependent differences in thrush movements, thrushes with more fat stores generally moved less and made more tortuous movements. However, lean thrushes moved similarly to fat thrushes early in the migration period, and the quantity and directedness of their movements only increased as migration progressed (Figures 4 and 5). Movements of fat thrushes during stopover remained consistent throughout the migratory period, perhaps reflecting an innate tendency to restrict diurnal movements when carrying fuel stores adequate for continued migration (Ktitorov et al. 2010).

Declining seasonal resources seems a plausible explanation for more apparent condition-dependent differences in movements later during the migration period. Food resources (especially fruit) were abundant and widely distributed early in migration and this allowed lean thrushes to secure adequate resources without making large exploratory movements (Ktitorov et al. 2010). However, although ground-dwelling arthropod abundance remained relatively consistent throughout the fall (Figure 6A), fruit resources declined rapidly (Figure 6B). In particular, the highly nutritious fruits of arrowwood and Virginia creeper, preferred fruits among songbird migrants on Block Island (Smith et al. 2007; Bolser et al. 2013), were essentially absent by the end of the migratory period (Figure 6B). Thrushes are highly omnivorous and rely extensively on fruit during fall migration on Block Island (Parrish 1997; Smith and McWilliams 2010) and, thus, may have been particularly sensitive to declining fruit abundance and nutritional quality of remaining fruits. We note, however, that although we monitored resource abundance at an appropriate scale (i.e., in an area encompassing most thrush

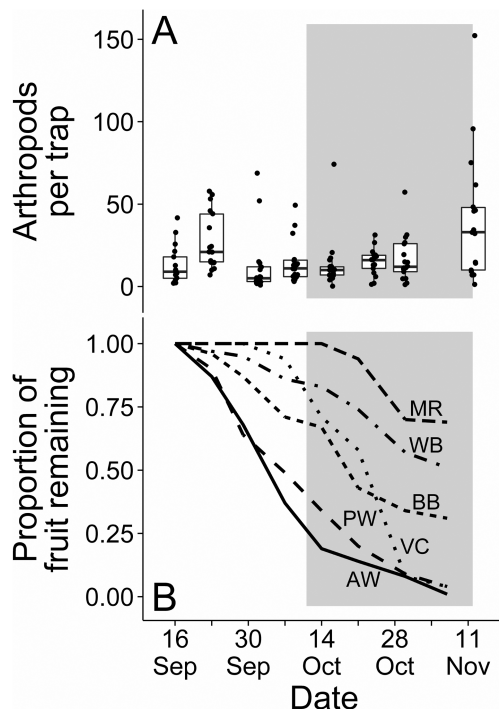


Figure 6

Change in (A) ground-dwelling arthropod and (B) fruit resource abundance on Block Island, RI, USA, during the 2010 fall migration. (A) Boxplots indicate the median and IQR (box) and whiskers extend 1.5 times beyond the IQR; raw data values are indicated by dots. (B) Lines indicate the median proportion of fruit remaining. The shaded area in each panel indicates when telemetered thrushes used the area. Fruit species abbreviations (see text for scientific names)—MR: multiflora rose; WB: winterberry; BB: bayberry; PW: pokeweed; VC: Virginia creeper; and AW: arrowwood.

movements), we cannot ascertain whether declining resource abundance precipitated these condition-dependent movements later in migration. Shortening day length may also have elicited the endogenous time program, increasing foraging activity (Jenni and Schaub 2003; Bayly 2006), which seemingly obligates more extensive movements as resources decline. Fat birds may have been capable of foraging locally and minimally to maintain fuel stores and thus responded less sensitively to declining food resources and their endogenous time program.

Lean thrushes sharply decreased the magnitude and scale of their daily movements as stopover progressed (Figure 4). The decrease in total movement and, in particular, increasingly localized movements of individual lean thrushes during their stopover are consistent with expectations and suggest that leaner thrushes identified a core foraging area of adequate quality as they transitioned from an initial exploratory period (Aborn and Moore 1997; Cohen et al. 2012). The transition to more tortuous movements similar to those of fatter thrushes suggests that lean thrushes were able to quickly acquire fuel during stopover, perhaps at an increased rate relative to fatter thrushes through adjusted foraging behaviors (e.g., Loria and Moore 1990, Wang and Moore 2005, Cohen et al. 2012). Although fat thrushes maintained a consistent scale of movement during stopover (Figure 5), they nonetheless decreased total movement comparably to lean thrushes (Figure 4). This decrease possibly represented a similar albeit attenuated search and settling pattern. Songbirds occasionally decrease foraging activity and fueling rates in the day(s) leading up to departure (e.g., Fransson 1998; Bayly 2006, 2007), but it is not a consistent syndrome (Lindstrom and Alerstam 1992; Dänhardt and Lindström 2001). Moreover, as food is not available ad libitum on stopover (Ktitorov et al. 2010), thrushes with large fuel stores presumably needed to forage to some extent even if intending to depart the initial night after release (e.g., Biebach 1985).

Condition dependence of thrush departure decisions

Fuel stores are posited to influence departure decisions especially when the departure location precedes the crossing of migratory barriers (Alerstam 1978; Jenni and Schaub 2003; Sandberg 2003). In agreement with this expectation, fat mass at release exerted a significant influence on the nightly decision to depart Block Island. The persistence of this effect throughout stopover, despite most stopovers lasting 4 or more days, is noteworthy given that all thrushes possessed ample fuel stores at release to make either the return flight to the mainland or the onward flight toward Long Island (Figure 1; Wang and Moore 1993; Woodrey and Moore 1997). That increased fuel stores at release positively influenced the nightly decision to depart suggests that leaner thrushes found Block Island suitable for stopover or perceived the ocean crossing as a barrier requiring additional fuel stores.

Stopover duration varied negatively with thrush fuel stores at release, an expected association that seems straightforward for a time-limited bird during migration. However, the association between fuel stores at arrival and stopover duration is often ambiguous (e.g., Salewski and Schaub 2007; Tsvey et al. 2007). We expect that resolving the typically small duration differences (i.e., 1–2 days) between fat and lean birds is complicated by the challenge of accurately determining when migrants arrive and their fuel stores on arrival. Nonetheless, studies purporting to know both arrival fuel stores and stopover duration with relative certainty provide equivocal results (e.g., Buler 2006; Chernetsov and

Muhkin 2006; Bolshakov et al. 2007; Tsvey et al. 2007; Goymann et al. 2010; Ktitorov et al. 2010; Matthews and Rodewald 2010b, Cohen et al. 2014). Patterns of fuel accumulation during stopover likewise play a role in determining stopover duration (Eikenaar and Schläpke 2013) but are similarly difficult to assess (e.g., Schaub et al. 2008; but see Bulyuk and Tsvey 2013; Schmaljohann et al. 2013). Stopover duration seems to us subject to myriad intrinsic and environmental influences, and the variable association with initial fuel stores is perhaps unsurprising (Jenni and Schaub 2003).

Stopover duration of migrating songbirds decreases consistently as migration proceeded in spring (e.g., Wang and Moore 1997; Dierschke and Delingat 2001; Matthews and Rodewald 2010b, Cohen et al. 2014) and fall (e.g., Ktitorov et al. 2010; Morganti et al. 2011; Andueza et al. 2013), presumably in response to increasing time constraints. However, we found no indication of a seasonal pattern in stopover duration. To our knowledge, the only other exception to this otherwise ubiquitous pattern of decreasing stopover duration with migration period was a study of Northern Wheatears (*Oenanthe oenanthe leucorhoa*) faced with a substantial migratory barrier that required, of most individuals, substantial fuel stores and favorable atmospheric conditions (Dierschke and Delingat 2001). This scenario fails to describe the situation for songbirds such as thrushes stopping over on Block Island. We speculate that the endogenous time program may have been less crucial with temperate migrant thrushes. Individuals later in the season conceivably were near the end of their migratory journey and perhaps largely freed from the endogenous time program. The time program is perhaps even less relevant for immature migrants with a reduced incentive to reach wintering areas early only to be displaced by more dominant adults (e.g., Marra 2000).

Fuel stores generally influenced thrush decisions to continue migration in a seasonally appropriate direction. However, the migratory dynamics of Block Island makes it reasonable to question whether thrush departures from Block Island represent true oriented migrations or extended landscape-level stopover movements (e.g., Mills et al. 2011; Taylor et al. 2011). For instance, most birds using Block Island as a stopover are immature birds that presumably have been displaced offshore after having failed to correct for wind drift (e.g., Baird and Nisbet 1960; Ralph 1978). Long Island and the mainland are both visible from Block Island on clear nights and within the maximum reported range of extended stopover movements by thrushes in the region (Taylor et al. 2011); reverse migrants can move on similar scales (Åkesson et al. 1996), and reverse migration may simply be a specific case of geographically constrained extended stopover (Ktitorov et al. 2010). Regardless of whether onward migration toward Long Island demonstrated the ability of some inexperienced thrushes to correct for displacement (Thorup et al. 2011), we suggest that variation in the timing of departures related to departure direction support the idea that seasonally appropriate departures represented true migratory movements.

Thrushes leaving toward Long Island left earlier in the night than reorienting birds. This is consistent with evidence that birds undertaking true migratory departures leave earlier in the night relative to those making reorientation or risk-sensitive movements at migratory barriers or landscape-scale stopover movements (Mills et al. 2011; Schmaljohann and Naef-Daenzer 2011; Smolinsky et al. 2013). Migrating birds may leave earlier in the night to maximize the time available for migration (Bolshakov et al. 2007) or to take advantage of available directional cues (Cochran et al. 2004; Muheim et al. 2006). Additional variation in departure times may

relate to duration of the current stopover, atmospheric conditions, and migrant motivation (Bulyuk and Tsvey 2006; Bolshakov et al. 2007; Bulyuk 2012) although our reduced sample of thrushes with recorded departures precluded a detailed investigation of this variation.

Environmental influences on thrush movements and departure decisions

We documented an inverse association between precipitation and diurnal movements. To our knowledge, no such influence of precipitation on movement dynamics during stopover has previously been documented. However, precipitation was relatively uncommon during the study (11% of days with monitoring), and only on half of those days did it rain for more than half of the daylight hours. We thus suggest precipitation played only a small role in modifying thrush movement behavior during stopover although it may play a more important role in birds that forage exclusively on (particularly aerial) arthropods. Nonetheless, the influence of precipitation seems far more relevant to departure decisions.

Thrushes distinctly avoided departing during precipitation. Measureable precipitation occurred on 27% of all monitored nights, yet only 1 out of 44 birds departed on a night with precipitation (a maintenance bird reorienting toward the mainland) and that bird left prior to the precipitation. This supports an important role of precipitation in modifying departure decisions (Richardson 1978; Dänhardt and Lindström 2001; Erni et al. 2002; Schaub et al. 2004; Van Belle et al. 2007; Tsvey et al. 2007; Morganti et al. 2011; Smolinsky et al. 2013) and is not surprising given that flying during precipitation likely imposes severe energetic and possibly survival costs on migrants (Schaub et al. 2004).

Birds that depart on nights with favorable wind directions can greatly reduce their energetic costs of flight (Richardson 1978; Liechti 2006). Interestingly, most such work supports a primary influence of wind speed rather than wind direction although tailwinds may be more important at migratory barriers (e.g., Åkesson and Hedenström 2000; Dänhardt and Lindström 2001; Dierschke and Delingat 2001; Tsvey et al. 2007; Morganti et al. 2011; Schmaljohann and Naef-Daenzer 2011). Birds can make migratory progress, even in headwinds, so long as wind speeds remain below migrant airspeeds. Thrushes preferentially departed Block Island on nights with lower average wind speeds. Thrushes typically maintain a consistent heading rather than correct for wind drift (Cochran and Wikelski 2005) and, in general agreement, the vanishing directions of thrushes in this study occasionally deviated considerably from their departure direction due to prevailing wind directions, at least for the 6–10 km we could detect their departures. Thrushes continuing migration to the southwest consistently selected light or weak tailwinds, whereas reorienting thrushes departed under considerably variable wind conditions.

CONCLUSIONS

The simultaneous release of individual migrants with manipulated fuel stores allowed us to directly test hypotheses about the condition dependence of behavioral decisions of songbirds during migratory stopover. Our experiments supported the hypotheses that thrushes with increased fat stores moved less and made less directed movements, that these differences in movements abate over the course of a given stopover, and that the condition-dependent differences in movements are accentuated in late-migrating individuals because of declining resource availability. Consistent lengths of stopover

throughout the migratory period suggested that time constraints may be less important in fall temperate migrants. With further regard to departure decisions, our results supported the hypothesis that birds with more substantial fat stores were more likely to resume migration earlier and in a seasonally appropriate direction relative to individuals released with little change in fuel stores. As expected, precipitation suppressed thrush movements during stopover and, more decisively, inhibited thrush departure. Departure decisions were influenced primarily by wind speed, although thrushes continuing migration in a seasonally appropriate direction indicated some preference for tailwinds. The pervasive influence of fuel stores on migrant stopover behavior underscores the importance of high-quality stopover sites and the central role of fuel acquisition in the dynamics, speed, and success of migration.

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