



INFLUENCE OF MOISTURE AND FOOD SUPPLY ON THE MOVEMENT DYNAMICS OF A NONBREEDING MIGRATORY BIRD (*PARKESIA NOVEBORACENSIS*) IN A SEASONAL LANDSCAPE

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ABSTRACT.—We radiotracked Northern Waterthrushes (*Parkesia noveboracensis*) in four habitats in Puerto Rico during two winters (i.e., January–April) in 2003 and 2004 to determine the ecological determinants of diurnal space use and overwinter site-persistence in this species. The majority of birds (69%) were sedentary and used a contiguous area within a single habitat over the winter period. A smaller percentage (31%) initially used a contiguous area within a single habitat but then permanently moved from that area to another disjunct location (mean = 418 m). Most of these movements were out of the two habitats (dry forest and Black Mangrove) that became the driest from January to mid-March and into wetter mangrove areas. The primary determinants of movement probability were moisture and food availability on each bird's home range. Foraging areas of birds that eventually moved were drier and had lower food availability than areas used by site-persistent individuals. The sites that these itinerant birds moved to were wetter and had higher food availability, which suggests that individuals moved in response to changing resources. Our results (1) indicate that habitats used by this species differ in suitability and (2) support previous findings that turnover rates within a habitat could serve as an indicator of habitat quality. The ability to predict behavioral responses of individuals to habitat conditions that vary across space and time is essential for understanding individual and population responses to habitat loss and the effects of a changing climate in the New World tropics. Received 17 October 2010, accepted 7 December 2010.

Key words: dry season, habitat quality, movement ecology, nonbreeding season, Northern Waterthrush, *Parkesia noveboracensis*.

Influencia de la Humedad y del Suministro de Alimentos sobre las Dinámicas de Movimiento de un Ave Migratoria No Reproductiva (*Parkesia noveboracensis*) en un Paisaje Estacional

RESUMEN.—Seguimos mediante transmisores de radio a individuos de *Parkesia noveboracensis* en cuatro ambientes en Puerto Rico durante dos inviernos (i.e., enero-abril) en 2003 y 2004 para establecer los determinantes ecológicos del uso del espacio diurno y la persistencia en sitios de invernada en esta especie. La mayoría de las aves (69%) fueron sedentarias y usaron un área contigua dentro de un único ambiente a lo largo del período invernal. Un porcentaje más pequeño (31%) usó inicialmente un área contigua dentro de un único ambiente pero luego se movió de modo permanente desde esta área a otro sitio disyunto (media = 418 m). La mayoría de estos movimientos fueron hacia afuera de los dos ambientes (bosque seco y manglar negro) que se tornaron los más secos desde enero hasta mediados de marzo y hacia áreas de manglar más húmedas. Los determinantes primarios de la probabilidad de movimiento fueron la humedad y la disponibilidad de alimento en el ámbito de hogar de cada ave. Las áreas de forrajeo de las aves que eventualmente se movieron fueron más secas y tuvieron menor disponibilidad de alimentos que las áreas usadas por individuos que persistieron en los sitios. Los sitios a los que estas aves itinerantes se movieron fueron más húmedos y tuvieron mayor disponibilidad de alimentos, lo que sugiere que los individuos se movieron en respuesta a recursos cambiantes. Nuestros resultados (1) indican que los ambientes usados por esta especie difieren en idoneidad y (2) apoyan resultados anteriores que indican que las tasas de recambio dentro de un ambiente pueden servir como un indicador de la calidad del hábitat. La habilidad para predecir las respuestas de comportamiento de los individuos a las condiciones del ambiente que varían a lo largo del espacio y del tiempo es esencial para entender las respuestas individuales y poblacionales a la pérdida de hábitat, y los efectos de un clima cambiante en el trópico del Nuevo Mundo.

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IN MIGRATORY BIRDS, nonbreeding-season events can have fitness consequences that occur during both the nonbreeding and the subsequent breeding season (Marra et al. 1998, Reudink et al. 2009) and play an important role in regulating populations (Sherry and Holmes 1996, Runge and Marra 2005). Despite this, there are still relatively few detailed studies of the determinants of spatial and social behavior of nonbreeding migratory songbirds (Greenberg and Salewski 2005). Studying how interactions between individuals and their environment drive space-use strategies can help explain patterns of distribution and abundance across space and time (Borger et al. 2006b, Nathan et al. 2008). Elucidation of the mechanisms that drive space-use decisions is essential for identifying the factors that limit and ultimately regulate populations.

Species of nonbreeding Neotropical–Nearctic migrant passerine birds are known to exhibit multiple strategies of overwinter space use. In one of the most frequently reported behaviors in nonflocking species, the majority of individuals remain site-persistent in a single contiguous home range throughout the winter while a subset of individuals exhibit “floating” or “wandering” behavior (Brown and Long 2007). The latter appear to be less site-attached and often move over a wide area that encompasses stable home ranges of conspecifics (Winker 1998).

Although the site-persistent segments of such populations are often well studied, the subset using alternative strategies is less well understood, mainly because the probability of resighting or recapturing wanderers is lower (Winker et al. 1990). Moreover, few studies have employed radiotransmitters to track patterns of space use in nonbreeding birds (Winker et al. 1990; Brown et al. 2000; Brown and Sherry 2006b, 2008; Townsend et al. 2010), and, as a result, few detailed descriptions of alternative space-use strategies exist and little is understood about the causes and consequences of wandering behavior.

Site-persistence behavior is known to vary across habitat types (Strong and Sherry 2000; Wunderle and Latta 2000; Latta and Faaborg 2001, 2002; Latta et al. 2003; Wunderle et al. 2010), and food availability has been proposed as a primary determinant of this variation (Sherry and Holmes 1996, Sherry et al. 2005). However, the movements of emigrants have rarely been tracked, and only a few studies have shown that individuals are less site-persistent in areas of low food availability (Johnson and Sherry 2001, Latta and Faaborg 2002). Quantifying these movements is essential for determining whether emigration or mortality explains the disappearance of these birds and, in the case of emigration, testing hypotheses regarding the role that food resources play in mediating site-persistence and movement patterns (Johnson and Sherry 2001, Brown and Sherry 2006a). Ultimately, our ability to explain distribution patterns in nonbreeding passerine birds will require a better understanding of the factors that affect both food abundance and how food drives space use.

In the tropics, invertebrate abundance varies over both space and time, and moisture is often a determinant of such variation (Janzen 1980, Tanaka and Tanaka 1982, Poulin et al. 1992, Studds and Marra 2007). Moisture levels vary across habitats and increase from thorn and dry forest to mangroves (Marra et al. 1998; Latta and Faaborg 2001, 2002). Moisture levels within habitats can also vary seasonally because of annual fluctuations in rainfall (Poulin et al. 1992). Although the relationship between moisture and invertebrate abundance has been established at the habitat level for

nonbreeding migratory birds, few studies have investigated the link between these two variables at the home-range level in a temporally explicit way (Studds and Marra 2007).

We examined the relationships between habitat conditions, food availability, and individual decisions of a migratory passerine over the nonbreeding season. Using radiotelemetry, we quantified patterns of space use and determined habitat-specific rates of overwinter site-persistence for the Northern Waterthrush (*Parkeisia noveboracensis*). We then examined how habitat moisture during the dry season is related to food availability and examined the role of these factors in mediating space-use decisions in Northern Waterthrushes. Specifically, we tested (1) whether food availability in late winter was correlated with habitat moisture; (2) whether food availability was a determinant of overwinter site-persistence; and (3) whether nonbreeding-season movements of individual birds tracked changes in resources.

METHODS

Study species.—The Northern Waterthrush is a paruline warbler that breeds in the northeastern United States, Alaska, and Canada and winters in Central America, northern South America, and the Caribbean (Eaton 1995). During the nonbreeding period, the species is site-faithful and solitary (Schwartz 1964, Lefebvre et al. 1994, Reitsma et al. 2002) and is considered a moist-habitat specialist (Wunderle and Waide 1993). Winter diet is composed of invertebrates (Lefebvre et al. 1992), and foraging occurs primarily at ground level (Schwartz 1964, Lefebvre et al. 1992).

Study sites.—We conducted our research at Roosevelt Roads Naval Station (18°20'N, 65°60'W) near Ceiba, on the east coast of Puerto Rico, during the period January–April in 2003 and 2004. The station occupies 3,464 ha, of which 1,612 are second-growth dry forest, 769 mangrove forest, and 1,083 developed (Landcover map of Naval Station Roosevelt Roads; Eagan, McAllister Associates, Lexington Park, Maryland). The developed areas comprise roads, an airstrip, residential areas, office complexes, commercial properties, and a seaport.

Our research was conducted in second-growth dry forest and three mangrove forest types. Each of the mangrove forest plots was dominated by a single species: Black Mangrove (*Avicennia germinans*), White Mangrove (*Laguncularia racemosa*), or Red Mangrove (*Rhizophora mangle*). Dry forest was a heterogeneous habitat with a more complex plant community dominated by Gumbo Limbo (*Bursera simaruba*), White Leadtree (*Leucaena leucocephala*), Honey Mesquite (*Prosopis juliflora*), and Lignum-Vitae (*Guaiacum officinale*) (Ewel and Whitmore 1973). Red Mangrove areas were directly adjacent to the coast and to lagoons and major drainages and occurred in pure stands, whereas Black Mangrove and White Mangrove formed mixed and single-species stands inland from Red Mangrove areas. Dry-forest sites were still further inland, but adjacent to mangroves. Additional mangrove areas present at Roosevelt Roads Naval Station that were only rarely used by Northern Waterthrushes included short-stature (<2 m) stands of Black Mangrove and stands of dead mangrove.

Study sites consisted of two White Mangrove sites 6.5 km apart, two Black Mangrove sites 1.5 km apart, two dry-forest sites 1.5 km apart, and one Red Mangrove site that was separated from the nearest dry-forest site by a 300-m band of salt flats interspersed

with sparse, short-stature Black Mangrove. Canopy heights within each site ranged from 3 to 20 m. All mangrove sites had standing water, usually <1 m deep in January, but water depth gradually decreased as the dry season progressed in spring toward April and May. Daily fluctuations in moisture levels infrequently occurred in coastal Red Mangrove areas during periods of exceptional tidal fluctuations. Dry-forest sites did not have standing water.

Radiotelemetry.—Northern Waterthrushes were captured in late January, mid-February, and early March. We erected 10 to 15 twelve-meter mist nets in each habitat type for a 2-day period from 0800 to 1600 hours AST. To avoid biases toward territorial or behaviorally dominant individuals, the birds were captured without the use of playbacks or other enticements. At the time of capture each was banded with a unique combination of two-colored leg bands and an aluminum U.S. Fish and Wildlife Service band. A 50- μ L blood sample was taken to determine sex, following the protocol of Griffiths et al. (1998). Ages were unknown, because methods for determining age in this species are not reliable during winter (Pyle 1997). Only individuals captured at least 1 h after sunrise were used, to avoid capturing animals in commute from a roost location and thereby maximize the probability that they were using the habitat in which they were captured (Smith et al. 2008). Each individual was fitted with a radiotransmitter with a unique frequency ($n = 75$; Holohil BD2-A, 0.74 g) using the leg-harness technique (Rappole and Tipton 1991). Transmitter life ranged from 3 to 4 weeks. Each year, we deployed 30 transmitters in late January, 30 in mid-February, and 15 in early March. During the February and March capture intervals, we attempted to recapture as many birds as possible that were initially captured and tracked during January in order to replace weak transmitters with new units to extend the tracking period of the same individuals. We radiotracked and measured home-range attributes of 75 Northern Waterthrushes in 2003 (21 males and 25 females) and 2004 (19 males and 18 females) within and across the four habitat types. We tracked three individuals in both years but used only their 2003 data for all analyses. Birds were tracked for periods of 7–70 days (mean = 32.3, median = 26 days).

Pilot data from 2002, when individuals were located three times a day, showed little change in location within a day once a bird arrived on its foraging area. To quantify space use, we therefore acquired one location per day for each individual during the tracking period. We collected location data throughout the day to reflect the full span of daylight hours, except for dawn and dusk periods when the majority of birds were commuting to distant roost sites (Smith et al. 2008). We used radio receivers (Fieldmaster 16; Advanced Telemetry Systems, Isanti, Minnesota) and 3-element Yagi antennas to relocate individuals with transmitters via homing. We approached as closely as possible without disturbing the bird (~10 m). The observer marked the location with a global positioning system (Garmin GPS 12) and estimated the distance and recorded the bearing from this point to the bird.

Overwinter site-persistence was defined by the persistence of a bird in a single, contiguous diurnal activity area. The permanent movement of a bird from one activity area to another discrete location was considered a midwinter home-range shift. Failure to detect a bird in its usual location suggested that it had dispersed. We then immediately initiated a wider search, but because the range of our transmitters was only ~100 m, we conducted our

initial search from hilltops directly upslope of mangrove and dry-forest study sites to find the bird's new location. In only four cases were we unable to relocate a disperser; we were able to confirm that the bird was still alive and carrying a transmitter in each of these cases because we could detect them while they moved to and from a coastal roost site (Smith et al. 2008).

We estimated home-range areas by using radiotelemetry locations for each bird to identify a core home-range area using fixed-kernel density estimation at a 50% isopleth (Borger et al. 2006a). We limited this analysis to birds that were tracked for ≥ 15 days ($n = 46$) to provide enough data for home-range characterization. Beyond 15 days, home-range size (log transformed) did not increase as days tracked increased ($F = 1.20$, $df = 1$, $P = 0.28$).

Repeated surveys of habitats to monitor dry-season effects.—To document seasonal changes in habitat conditions, we monitored 16 random points arranged in a regular grid covering 2 ha at one site in each of the four habitats where we made initial captures of Northern Waterthrushes for radiotracking. We conducted the surveys in mid-January and again in mid-March. At each point we measured water volume (cm^3), tree leaf loss, and arthropod food availability.

We calculated water volume in the three mangrove habitats by estimating water coverage in a 5-m circular plot using the point-intercept technique (Bonham 1989) and measuring the average water depth in the plot. We measured leaf loss by selecting the tree branch closest to the point and counting the number of green leaves on the branch. To measure food availability at these points, we used a timed, direct search of the ground substrate within a 0.2-m² quadrat (Strong and Sherry 2000). Each search was divided into a passive and active period. The first 3 min were spent visually searching the sample area, and during the subsequent 2 min the substrate (usually leaf litter) was overturned to expose hidden prey. The active search method was used because the Northern Waterthrush is an active leaf-tosser during foraging (Schwartz 1964, Post 1978). All invertebrates encountered were classified by taxonomic order, and their length (mm) was measured in the field. Active and passive periods were combined for analysis, and biomass was calculated using published length–weight regressions for Jamaican arthropods (Johnson and Strong 2000). Previous research using emetic sampling documented the winter diet of Northern Waterthrushes in Panama at a similar coastal study site (Lefebvre et al. 1992, Poulin et al. 1994). We restricted our samples to arthropod orders and size classes that were a known component of Northern Waterthrush diets (Gastropoda, Decapoda, Araneae, Odonata, Isoptera, Hemiptera, Homoptera, Neuroptera, Coleoptera, Lepidoptera, and Hymenoptera).

Patterns of moisture at radiotelemetry locations.—We used an index of moisture derived from satellite imagery to measure moisture patterns at locations within our study area. Two representative scenes of 30-m-resolution Landsat +ETM imagery were used to quantify habitat conditions in early January (9 January 2001) at the start of the dry season and in late March (27 March 2000) near the end of the dry season. Although the scenes that we used did not correspond to the actual years of our field work, habitat coverage within the study sites was identical (Landcover map of Naval Station Roosevelt Roads), and 2000 and 2001 were years with typical annual rainfall patterns: a pronounced dry season occurs between January and March following a much wetter period

between September and December. Availability of satellite imagery is limited by cloud cover in the study area and by the Scan Line Correction error, which makes it difficult to use Landsat 7 ETM+ scenes after July 2003 (Markham et al. 2004).

To derive an index of wetness from the Landsat scene, the tasseled-cap transformation was performed using ENVI, version 4.4 (ITT Corporation, White Plains, New York). This transformation uses a standard series of coefficients to create weighted sums of spectral bands, resulting in a reduced number of bands that explain >95% of image variation (Crist and Cicone 1984). The first three resultant bands are the most frequently used and correspond to brightness, greenness, and wetness (Crist and Kauth 1986). Here, we use the wetness component as a relative measure of soil moisture within Northern Waterthrush home ranges. This component estimates the amount of moisture held by vegetation and soil and is calculated by contrasting infrared spectral bands with the sum of visible and near-infrared spectra (Crist and Cicone 1984). Previous work has shown that this index corresponds well to temporal and spatial variation of soil (Ordoyne and Friedl 2008) and canopy foliar moisture (Toomey and Vierling 2005), and that soil moisture and canopy moisture are closely correlated (Harris et al. 2004, Williams and Albertson 2004). To calculate wetness on Northern Waterthrush home ranges, we extracted these values for all raster cells corresponding to telemetry locations and calculated a mean wetness value for each home range.

Food availability at radiotelemetry locations.—When a bird was located, prey availability at its location was quantified using a timed, direct search of the ground substrate within a 0.2-m² quadrat as described above. We attempted to take samples in the exact location where the bird was found, but if the bird remained in that location, we placed the sample site as close as possible to the bird without disturbing it (always within 10 m) and in the same substrate type that the bird was using. Foraging areas in all habitat types were on the ground in leaf litter, mud, or mangrove pneumatophores. Home-range food availability was measured for 74 individuals; 5 to 36 (mean = 14, median = 12) samples were taken from each home range.

Statistical analyses.—To examine the effects of changing habitat conditions within individual territories on food availability, we used classification and regression-tree analysis (CART). We chose CART analysis because preliminary data-screening revealed nonlinear and heteroscedastic relationships that violated assumptions of standard multiple regression (De'ath and Fabricius 2000). We built a series of regression trees of increasing complexity based on two predictor variables to model early- and late-winter food availability on individual home ranges for birds that were tracked during January (at the beginning of the dry season) and March (at the end of the dry season). Predictor variables were tasseled-cap wetness index and change in tasseled-cap wetness index between January and March. We used tenfold cross-validation for each tree to determine the appropriate tree complexity (Breiman et al. 1984).

We used known-fate time-to-event analysis (Kaplan and Meier 1958) with staggered entry (Pollock et al. 1989) in Program MARK (White and Burnham 1999) and an information-theoretic approach (Burnham and Anderson 2002) to examine the influence of home-range conditions and time on Northern Waterthrush site-persistence. We included predispersal home-range food availability, March tasseled-cap wetness index, change in tasseled-cap

wetness index between January and March, sex, and time as possible predictors of overwinter site-persistence. The time component in the analysis was represented by five 2-week periods beginning on 24 January and ending on 4 April.

We assembled a set of candidate models that reflected *a priori* hypotheses to explain site-persistence. On the basis of previous work, we hypothesized that food availability is a direct driver of site-persistence (Lefebvre and Poulin 1996, Johnson and Sherry 2001, Borgmann et al. 2004, Kwit et al. 2004, Sherry et al. 2005). Although it may not directly drive patterns of space use, we included wetness in candidate models because wetness may influence unmeasured ecological components that affect site-persistence such as predators (Rappole et al. 1989), parasites and disease (Latta 2003), or competition (Greenberg 1986). To select the best model(s) for inference, we ranked the set of candidate models using Akaike's information criterion corrected for small sample sizes (ΔAIC_c ; Burnham and Anderson 2002). The strength of evidence for each model was evaluated using AIC_c weights, and the relative importance of each explanatory variable was assessed using cumulative AIC_c weights (the sum of all candidate model weights that included the variable; Burnham and Anderson 2002). Statistics are reported as mean \pm SE throughout.

RESULTS

Radiotracked Northern Waterthrushes exhibited two patterns of diurnal space use. The majority of birds were site-persistent over winter and used a contiguous area within a single habitat (69%; $n = 55$). The remainder (31%; $n = 25$) used a contiguous area within a single habitat initially but then permanently moved to a different area. There was no difference between sexes in their tendency to remain site-persistent ($\chi^2 = 2.99$, $df = 1$, $P = 0.10$). Home-range shifts were at a relatively fine spatial scale (418 ± 60.89 m) but still were much greater than overall mean day-to-day movements (70 ± 2.42 m). Two birds that shifted their home ranges oscillated between their old and new locations within the first few days of the transition before permanently settling into their new locations.

Kernel home-range estimates for site-persistent birds and those that shifted their activity areas were not significantly different (persistent: mean = 0.32 ± 0.056 ha, $n = 40$; itinerant, including both pre- and postmovement locations: mean = 0.99 ± 0.31 ha, $n = 14$; Wilcoxon signed-rank $z = -1.88$, $P = 0.061$). Movement events showed no strong temporal pattern, occurring from early February through the end of March (mean date, 2003: 21 February \pm 3.53 days; mean date, 2004: 24 February \pm 3.93 days). Movements in both years were most frequent during early March, with 4 of 14 birds (28.6%) moving on 4 and 5 March 2003 and 4 of 14 birds moving on 7 and 8 March 2004.

Within-season home-range shifts were habitat-dependent. Few individuals moved from White Mangrove (5.5%, 1 of 18) or Red Mangrove (6.6%, 1 of 15), and these birds moved to different sites within the same habitat. Of the birds that initially used Black Mangrove, 48% (11 of 23) also moved to wetter sites within the same habitat. In dry forest, 40% of birds that initially used this habitat moved (12 of 30). Of the 12, two shifted to dry forest and 10 moved to Red Mangrove.

Patterns of habitat change.—At the random points within each habitat that we monitored in mid-January and again in

mid-March, standing water volume in each of the three mangrove habitats declined significantly ($P < 0.05$). The magnitude of change varied by habitat. Black Mangrove experienced a significantly greater decrease ($-100 \pm 9.13\%$) in standing water than did White Mangrove ($-36.9 \pm 3.68\%$; Wilcoxon signed-rank $z = -2.8$, $P = 0.005$) and Red Mangrove ($-63.4 \pm 7.32\%$; Wilcoxon signed-rank $z = -3.37$, $P < 0.001$). There was no significant year effect on the magnitude of decline across these habitats (Wilcoxon ranked-sum $z = -1.68$, $P = 0.098$).

The number of leaves declined significantly in all four habitats ($P < 0.05$) as well, but the magnitude of change varied by habitat ($\chi^2 = 8.85$, $df = 3$, $P = 0.031$). Dry forest had greater leaf loss ($45.9 \pm 5.61\%$) than Black Mangrove ($18.1 \pm 7.93\%$), White Mangrove ($11.9 \pm 7.62\%$), and Red Mangrove ($15.7 \pm 8.28\%$). There was no year effect on the magnitude of decline across these habitats (Wilcoxon ranked-sum $z = -0.61$, $P = 0.54$).

Changes in food availability also varied by habitat. Food availability declined significantly in dry forest (January mean = 8.8 ± 2.34 mg dry weight/0.1 m²; March mean = 3.7 ± 0.65 mg/0.1 m²; Wilcoxon signed-rank $z = -2.07$, $P = 0.038$) and Black Mangrove (January mean = 6.7 ± 1.07 mg dry weight/0.1 m²; March mean = 2.9 ± 0.95 mg/0.1 m²; Wilcoxon signed-rank $z = -2.44$, $P = 0.015$). Food availability increased significantly in White Mangrove (January mean = 9.3 ± 1.83 mg dry weight/0.1 m²; March mean = 19.5 ± 4.03 mg/0.1 m²; Wilcoxon signed-rank $z = 2.42$, $P = 0.016$) but remained stable in Red Mangrove (January mean = 3.9 ± 1.25 mg dry weight/0.1 m²; March mean = 7.9 ± 5.81 mg/0.1 m²; Wilcoxon signed-rank $z = 0.52$, $P = 0.61$). There was no significant year effect on the change in food availability in these habitats (dry forest, Wilcoxon ranked-sum $z = -0.56$, $P = 0.57$; Black Mangrove, Wilcoxon ranked-sum $z = -1.05$, $P = 0.29$; White Mangrove, Wilcoxon ranked-sum $z = -0.30$, $P = 0.76$; Red Mangrove, Wilcoxon ranked-sum $z = -1.85$, $P = 0.072$).

Patterns of moisture at radiotelemetry locations.—Satellite-derived wetness indices on Northern Waterthrush home ranges ranged from -92 to -27 (a unitless measure; drier conditions indicated by increasingly negative values). Overall, sites used by Northern Waterthrushes became significantly drier between January (mean = -46.06 ± 3.09 and March (mean = -51.58 ± 1.56 ; Wilcoxon signed-rank $z = -2.80$, $P < 0.005$; $n = 86$). In January, Red Mangrove was significantly wetter than all other habitats ($P < 0.008$; pairwise Wilcoxon ranked-sum tests with Bonferroni correction, $\alpha = 0.008$ to achieve an overall error rate of 0.05) and White Mangrove was significantly wetter than dry forest ($P < 0.008$). Between January and March, Red Mangrove and White Mangrove dried significantly (Wilcoxon signed-rank test, Red Mangrove: January mean = -20.04 , March mean = -46.08 , $z = -3.29$, $P < 0.001$; White Mangrove: January mean = -33.97 , March mean = -44.10 , $z = -3.34$, $P < 0.001$), whereas Black Mangrove and dry forest did not (Wilcoxon signed-rank test, Black Mangrove: January mean = -46.10 , March mean = -42.93 , $z = -0.40$, $P = 0.69$; dry forest: January mean = -61.04 , March mean = -60.16 , $z = -1.39$, $P = 0.17$). By March, all three mangrove habitats were equally dry (pairwise Wilcoxon ranked-sum tests at $\alpha = 0.008$ to achieve an overall error rate of 0.05, $P > 0.008$ for all comparisons) but still remained significantly wetter than dry forest ($P < 0.008$ for all comparisons).

Regression-tree analysis of home-range food availability.—There was no relationship between the wetness index and food

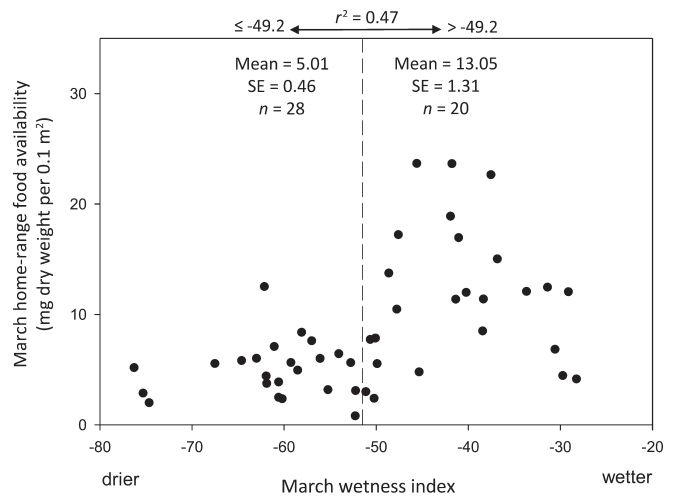


FIG. 1. Results from CART analysis of March Northern Waterthrush home-range food availability for the two-node tree size selected through cross-validation. The scatterplot illustrates the response of food availability to the March tasseled-cap wetness index. The vertical dotted line shows the wetness index value that best explained variation in food availability ($r^2 = 0.47$). The lower threshold value of the March wetness index is less than or equal to -49.2 (mean food availability = 5.01 ± 0.46 [SE]; $n = 28$). The upper threshold is >49.2 (mean food availability = 13.05 ± 1.31 ; $n = 20$).

availability ($r^2 = 0.01$) at the beginning of the dry season in January, which suggests that there was no strong variation in food availability among home ranges in different habitats. By March, however, during the late dry season, we found a nonlinear relationship between food availability and the home-range moisture index that indicated higher food availability in wetter locations. Cross validation of models produced by regression-tree analysis revealed that the model size that minimized relative error was also the simplest, with just two nodes and one variable: March wetness index. This final model explained 47% percent of the variation observed in food availability ($r^2 = 0.47$; Fig. 1). With two nodes in the model, this variation was partitioned at a single wetness-index value (-49.2). This value represents a threshold below which mean values of food availability are low at drier values (mean = 5.01 mg/0.1 m² ± 0.46 ; $n = 28$) and higher at wetter values above this threshold (mean = 13.05 mg/0.1 m² ± 1.31 ; $n = 20$).

Determinants of site-persistence.—Model rankings from known-fate analysis using AIC_c did not identify a single most parsimonious model. Of the six supported models, one had $\Delta AIC_c < 2$ and four had $\Delta AIC_c < 4$ (Table 1). All of these models included home-range food availability as a predictor of site-persistence. As a result, the variable importance weight of food availability was near 1.0 (0.99; Table 2), which indicates that it has high importance as a predictor compared with other variables in the candidate model set. In all models that included food availability, the 95% confidence interval of the coefficient for food availability excluded zero. None of the supported models included a time-dependent component of site-persistence probability, which means that dispersal events occurred throughout the dry season and showed no clear pattern with respect to time.

TABLE 1. Results of models that evaluated the effects of different variables on the probability of overwinter site-persistence (S). Analyses were performed with Program MARK. Models are ranked by ascending ΔAIC_c ; w_i is the model weight and N_p is the number of unique parameters that are estimated from each model. Parameters: food availability (food), March home-range wetness index (wetness), change in wetness index between January and March (change), sex, and time.

| Model | ΔAIC_c | w_i | N_p |
|---|----------------|-------|-------|
| $S_{\text{food} + \text{change}}$ | 0.00 | 0.348 | 3 |
| S_{food} | 1.06 | 0.205 | 2 |
| $S_{\text{food} + \text{wet} + \text{change}}$ | 2.05 | 0.125 | 4 |
| $S_{\text{food} + \text{wet}}$ | 2.95 | 0.079 | 3 |
| $S_{\text{time} + \text{food}}$ | 3.29 | 0.067 | 6 |
| $S_{\text{food} + \text{wet} + \text{change} + \text{wet} \times \text{change}}$ | 3.87 | 0.050 | 5 |
| $S_{\text{food} + \text{sex} + \text{wet} + \text{change} + \text{wet} \times \text{change}}$ | 5.27 | 0.025 | 6 |
| $S_{\text{time} + \text{food} + \text{sex} + \text{wet} + \text{change} + \text{wet} \times \text{change}}$ | 8.11 | 0.006 | 10 |
| $S_{\text{wet} + \text{change}}$ | 8.76 | 0.004 | 3 |
| S_{wet} | 9.68 | 0.003 | 2 |
| S_{change} | 9.87 | 0.003 | 2 |
| $S_{\text{time} + \text{sex}}$ | 10.14 | 0.002 | 6 |
| $S_{\text{wet} + \text{change} + \text{wet} \times \text{change}}$ | 10.78 | 0.002 | 4 |
| $S_{(.)}$ | 10.97 | 0.001 | 1 |
| $S_{\text{sex} + \text{wet} + \text{change} + \text{wet} \times \text{change}}$ | 12.78 | 0.001 | 5 |
| S_{time} | 12.80 | 0.001 | 5 |

Because a range of models in the candidate set were supported, we used model averaging to predict the effect of varying levels of home-range food availability on the probability of site-persistence. The resultant estimates (Fig. 2) indicate that as food availability increased, the probability of remaining site-persistent also increased.

Evidence for resource tracking: Moisture and food availability at the home-range level.—For birds that shifted their home range midseason, the areas that they moved to had significantly higher food availability ($9.0 \pm 1.28 \text{ mg}/0.1\text{m}^2$) than the areas they abandoned ($5.5 \pm 1.22 \text{ mg}/0.1\text{m}^2$; Wilcoxon signed-rank $z = -1.73$, $P = 0.044$, $n = 17$; Fig. 3A). Site-persistent birds had significantly higher mean food availability ($9.4 \pm 0.799 \text{ mg}/\text{m}^2$; $n = 54$) within their home ranges as compared with the foraging areas that home-range-shifting birds moved from ($5.5 \pm 1.22 \text{ mg}/0.1\text{m}^2$; Wilcoxon ranked-sum $z = -3.08$, $P = 0.002$, $n = 23$). Food availability in areas that home-range-shifting birds moved to was not significantly different from that in the home ranges of site-persistent birds when compared at the same time of year, in March (Wilcoxon ranked-sum $z = -0.75$, $P = 0.45$).

TABLE 2. Variable importance weights (Σw_i) obtained by summing AIC_c weights for each model in which the predictor variable was found.

| Predictor variable | Σw_i |
|---|--------------|
| Food availability | 0.99 |
| Δ Wetness January–March | 0.56 |
| March wetness | 0.30 |
| Sex | 0.11 |
| March wetness \times Δ wetness January–March | 0.08 |

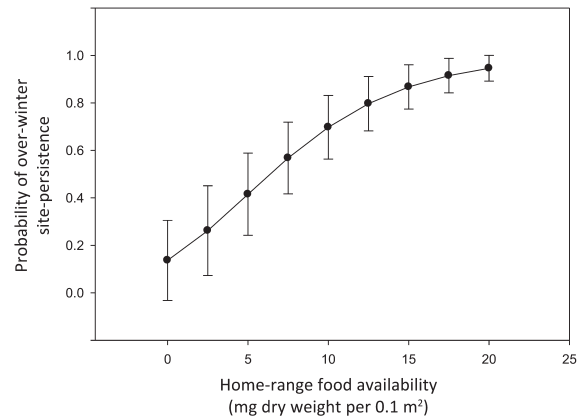


FIG. 2. Model-averaged probability of overwinter site-persistence (\pm SE) of Northern Waterthrushes in Puerto Rico estimated for different levels of home-range food availability.

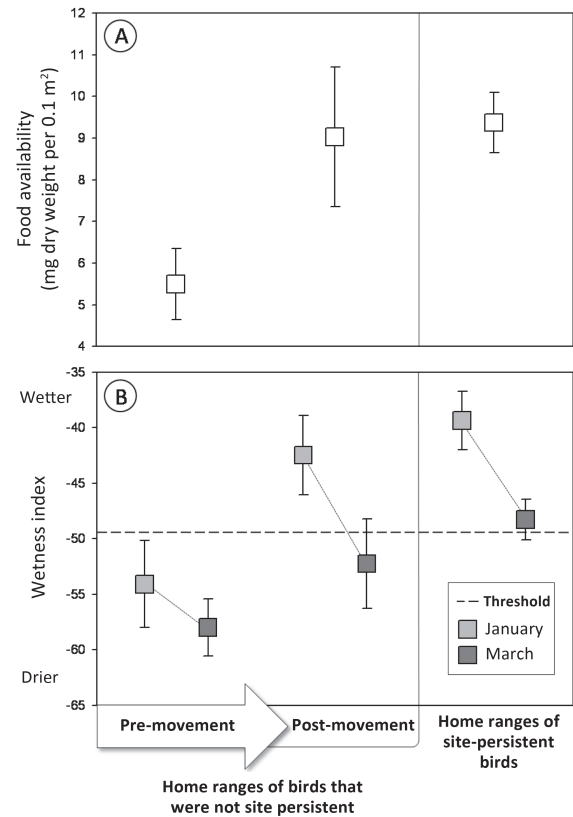


FIG. 3. Wetness index and food availability values for home ranges of Northern Waterthrushes in Puerto Rico that were site-persistent versus those that were not. Premovement values represent sites departed from, and postmovement values represent sites where these birds subsequently settled. (A) Food availability (mean \pm SE) of areas used by site-persistent ($n = 54$) and non-site-persistent Northern Waterthrushes both before and after shifting their home range ($n = 23$). (B) March wetness values (mean \pm SE) in the same areas for the same individuals. The horizontal dotted line indicates the wetness index threshold value resulting from CART analysis (Fig. 1) that best explained variation in food availability.

Wetness values in areas that were abandoned by home-range-shifting birds (January mean = -59.01 ± 5.20 ; March mean = -57.99 ± 2.58) were significantly drier than those in the home ranges of site-persistent birds (January mean = -43.21 ± 3.68 ; March mean = -48.99 ± 1.83) in both January (Wilcoxon ranked-sum $z = -2.88$, $P = 0.0038$) and March (Wilcoxon ranked-sum $z = -2.63$, $P = 0.008$; Fig. 3B). The areas to which home-range-shifting birds moved were wetter in both January (mean = -46.91 ± 6.21) and March (mean = -52.24 ± 4.01) than the areas they departed from (January mean = -59.77 ± 5.07 ; March mean = -57.40 ± 3.26), but these differences were significant for the January period only (Wilcoxon signed rank, January: $z = -2.38$, $P = 0.018$; March: $z = -1.13$, $P = 0.26$). Wetness in the areas to which home-range-shifting birds moved did not differ significantly from that in the home ranges of site-persistent birds in either January or March (Wilcoxon ranked sum, January: $z = -1.12$, $P = 0.263$; March: $z = -0.581$, $P = 0.558$).

DISCUSSION

Our data suggest that intraseasonal movements of Northern Waterthrushes are determined by food availability, which is in turn determined by moisture levels. The relationship between the satellite-derived wetness index and food availability suggests a nonlinear threshold effect in which food availability declines dramatically at a certain level of dryness. Northern Waterthrushes moved from areas that had mean wetness values below this threshold, which provides evidence that habitat conditions (i.e., moisture), food availability, and space-use decisions are linked.

We found additional evidence for the role of late-winter habitat conditions in determining space-use decisions: non-site-persistent birds consistently moved to sites that were both wetter and offered greater food availability than the places they had abandoned. Furthermore, the two habitats that birds left most frequently—dry forest and Black Mangrove—showed significant declines in food availability between January and March. These results suggest that individuals made movements in response to habitat conditions that deteriorated as the winter progressed. Resource tracking over space and time has previously been documented on a population level by demonstration of changes in bird density that correspond to changes in resources, particularly in frugivorous birds (Johnson and Sherry 2001, Renton 2001, Telleria and Perez-Tris 2003, Borgmann et al. 2004, Brown and Sherry 2006a). But demonstration of resource tracking by individually marked birds has only rarely been done (Wunderle et al. 2010), despite the importance of individual-based studies for revealing the mechanism behind seasonal changes in density.

Our results support the anecdotal observations of within-season movements from previous studies of the Northern Waterthrush during the nonbreeding season. Both Schwartz (1964) and Russell (1980) reported that Northern Waterthrushes abandoned dry forest areas when the forests became visibly desiccated, and Reitsma et al. (2002) documented changes in Northern Waterthrush density that corresponded to water-level fluctuations in a Black Mangrove study site. Finally, Lefebvre and Poulin (1996), working at two separate mangrove sites on both sides of the Isthmus of Panama, observed that Northern Waterthrush density increased at one mangrove study site as it became wetter during the study period but declined at the other as the site became drier.

They suggested that facultative movements may be occurring at a regional scale, but they were unable to test this hypothesis because they did not follow birds beyond the study-site boundaries. Our results suggest that, as hypothesized by Lefebvre and Poulin (1996), changes in density are moisture-dependent. However, radiotelemetry revealed that movements at our study sites were not at the broad scale suggested by these authors, all dispersal distances being <1 km.

All home-range shifts were characterized by single movements to a new home-range area where birds remained for the rest of the study period. Shifts were staggered over time, which suggests that either (1) some individuals showed a lag in their response to habitat change or (2) the rate of habitat change was heterogeneous across space. The shifts that we observed are distinct from “floating,” the most common alternative space-use strategy reported for Neotropical migratory birds during the nonbreeding season. Northern Waterthrush movements were more akin to the “itinerancy” (Moreau 1972) described in Palearctic–Afrotropical migratory birds wintering in the seasonal landscapes of Africa. In the latter system, regional changes in bird density are correlated with shifting rainfall patterns and it is hypothesized that birds in these systems are making large-scale midwinter movements to track changing resources (Jones 1998). Although the movements of Northern Waterthrushes are at a much finer scale, the seasonal changes that drive these movements are similar to those observed in these African systems.

Limited evidence suggests that individual birds’ movement strategies may remain stable from year to year. Two birds tracked in both study years used the same disjunct areas and made home-range shifts in the same sequence by making a single movement as the dry season progressed. Patterns of space use may remain stable from year to year because the patterns of local habitat change in response to the dry season also remain consistent. Our results show that, for example, as dry forests desiccate and trees lose their leaves, Red Mangrove, which was formerly inundated by water, begins to dry and more of the habitat becomes suitable because more ground is exposed. Birds respond to these changes in habitat suitability by making within-season movements. Individuals moved to areas that could support only low densities of Northern Waterthrushes prior to the dry season because standing water covered most of the habitat. As more ground substrate is exposed during the progression of the dry season, these areas may actually have the capacity to support higher Northern Waterthrush densities. The same pattern was true for birds moving within Black Mangrove. Birds moved from the edges of a basin, where we documented the total disappearance of standing water, toward its wetter central drainage as it dried. Conversely, White Mangrove, where birds were primarily sedentary, had a different flooding pattern. This habitat was characterized by alternating pools and raised islands of pneumatophores and leaf litter so that even in its wettest period, exposed foraging areas at ground level persisted.

We have shown that in shifting their home range, birds move to sites with greater moisture and food availability, and that the attributes of these new areas are similar to those of site-persistent individuals. The question that remains is whether this alternative space-use strategy affects the physical condition and survival of individuals. If there are benefits to remaining site-persistent during late winter, sites that allow residents to be sedentary may be

limiting and initial settlement of birds may be determined by competitive interactions (Marra 2000, Studds and Marra 2005, Smith et al. 2011). Additional research on how climate affects habitat conditions and the condition, survival, and behavior of individual birds is needed to understand the effect of changing habitat conditions on avian demography throughout the annual cycle (Sillett et al. 2000).

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