

Moisture as a determinant of habitat quality for a nonbreeding Neotropical migratory songbird

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Abstract. Identifying the determinants of habitat quality for a species is essential for understanding how populations are limited and regulated. Spatiotemporal variation in moisture and its influence on food availability may drive patterns of habitat occupancy and demographic outcomes. Nonbreeding migratory birds in the neotropics occupy a range of habitat types that vary with respect to moisture. Using carbon isotopes and a satellite-derived measure of habitat moisture, we identified a moisture gradient across home ranges of radio-tracked Northern Waterthrush (*Seiurus noveboracensis*). We used this gradient to classify habitat types and to examine whether habitat moisture correlates with overwinter mass change and spring departure schedules of Northern Waterthrush over the late-winter dry season in the tropics. The two independent indicators of moisture revealed similar gradients that were directly proportional to body mass change as the dry season progressed. Birds occupying drier habitats declined in body mass over the study period, while those occupying wetter habitats increased in body mass. Regardless of habitat, birds lost an average of 7.6% of their mass at night, and mass recovery during the day trended lower in dry compared with wet habitats. This suggests that daily incremental shortfalls in mass recovery can lead to considerable season-long declines in body mass. These patterns resulted in consequences for the pre-migratory period, with birds occupying drier habitats having a delayed rate of fat deposition compared with those in wet habitats. Taken together with the finding that males, which are significantly larger than females, are also in better condition than females regardless of habitat suggests that high-quality habitats may be limited and that there may be competition for them. The habitat-linked variation in performance we observed suggests that habitat limitation could impact individual and population-level processes both during and in subsequent periods of the annual cycle. The linkage between moisture and habitat quality for a migratory bird indicates that the availability of high-quality habitats is dynamic due to variation in precipitation among seasons and years. Understanding this link is critical for ascertaining the impact of future climate change, particularly in the Caribbean basin, where a much drier future is predicted.

Key words: body condition; body mass; habitat quality; migratory birds; nonbreeding winter habitat; Northern Waterthrush; Roosevelt Roads Naval Station, Puerto Rico; *Seiurus noveboracensis*.

INTRODUCTION

Climate and, more specifically, temperature and moisture, are among the most fundamental parameters that determine the composition and distribution of habitats (Holdridge 1967) and play an important role in determining resource abundances for organisms at higher trophic levels (Janzen and Schoener 1968, Karr and Freemark 1983, Bale et al. 2002). In lowland tropical regions, temperature at a given location is relatively stable (Janzen 1967). In comparison, moisture can vary considerably over space, seasonally, and across years due to geographic and seasonal patterns (Karr and

Freemark 1983, Murphy and Lugo 1986). Such variation may differentially impact the plant and invertebrate communities that comprise the habitats higher trophic level organisms occupy and may ultimately play a role in driving variation in demographic traits of these species.

Variation in moisture over time and space can have important impacts on populations by regulating food supplies (White 2008). In particular, studies in tropical environments that experience rainfall seasonality suggest a general pattern that wetter locations have higher food resources and that these differences in food resources can have consequences on individual condition and survival (Dunham et al. 2004, Madsen et al. 2006, Valeix et al. 2008). While moisture may vary temporally (i.e., across years and seasons) and affect all members of a population equally, moisture availability also varies spatially (i.e., within and among habitat types) and can result in consequences for different components of a population and ultimately play a role in population

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limitation and regulation (Johnson and McIlwee 1997, Studds and Marra 2007).

Neotropical migratory birds are an excellent taxonomic group to study the role of moisture in determining habitat quality because a single species often occupies a broad range of habitats that vary considerably with respect to moisture. Previous studies working across a range of habitats have demonstrated that insectivorous Neotropical migratory birds that occupy drier nonbreeding habitat types show lower overwinter site fidelity (Wunderle and Latta 2000, Latta and Faaborg 2001, 2002), declining physical condition and survival (Marra et al. 1998, Marra and Holmes 2001, Latta and Faaborg 2002, Brown and Sherry 2006, Johnson et al. 2006), delayed departure for breeding grounds (Marra et al. 1998), and delayed breeding initiation in the subsequent breeding season (Marra et al. 1998, Norris et al. 2004, Runge and Marra 2005, Reudink et al. 2009), suggesting that winter habitat quality plays a critical role in population regulation (Sherry and Holmes 1996, Runge and Marra 2005). Habitats are often classified a priori into patches of homogeneous types. Few studies of nonbreeding migratory birds have classified habitats a posteriori based on measures of ecologically relevant habitat features to better reflect how study organisms perceive habitats. While moisture is suggested as a determinant of habitat quality, few of these studies specifically measured moisture at the scale of individual home ranges to examine patterns of variation within and among habitats that may in turn influence food availability and an individual's physical condition.

In this study, we examine the role of moisture in driving arthropod availability and the physical condition and performance of the Northern Waterthrush (*Seiurus noveboracensis*) across four habitat types and over diurnal and seasonal timescales. We quantify moisture levels on the home ranges of radio-tracked birds occupying the four different habitat types using satellite imagery and a stable carbon isotope index of habitat moisture assessed from a blood sample from these radio-marked birds. To assess changes in body condition we quantify (1) overnight mass loss and daytime body mass recovery and (2) seasonal changes in body mass of Northern Waterthrush across the habitat moisture gradient. Finally, we assessed impacts of changes in body condition on the timing of spring migration.

METHODS

Species description and study area

The Northern Waterthrush is a paruline warbler that breeds throughout Canada, the northeastern United States, and Alaska and spends the nonbreeding period in the neotropics in Central America, northern South America, and the Caribbean (Eaton 1995). During the nonbreeding period the Northern Waterthrush is site faithful and solitary during the day (Schwartz 1964, Lefebvre et al. 1994, Reitsma et al. 2002) and is

considered to be a moist-habitat specialist, occurring in its highest recorded densities in mangroves (Wunderle and Waide 1993). The occupation of exclusive nonbreeding territories was documented in one study (Schwartz 1964) but others have found that home ranges overlap (Lefebvre et al. 1994, Reitsma et al. 2002). Evidence from our study sites indicates that at least some individuals maintain exclusive territories (Smith 2008). Foraging occurs primarily at ground level (Schwartz 1964, Lefebvre et al. 1992), and winter diet is composed of invertebrates (Lefebvre et al. 1992, 1994).

We conducted this research at Roosevelt Roads Naval Station (18°20' N, 65°60' W) near Ceiba, on the east coast of Puerto Rico during January–April 2002–2004. Of the total 3464 ha that compose the station, 1612 ha are second-growth dry forest, 769 ha are mangrove forest, and 1083 ha are developed (GIS data; Eagan, McAllister and Associates, *unpublished data*). Developed areas are composed of roads, an airstrip, residential areas, office complexes, commercial properties, and a ship port.

We worked in four habitat types including 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 (*Languncularia racemosa*), and red mangrove (*Rhizophora mangle*). Dry forest was a heterogeneous habitat with a more complex plant community dominated by *Bursera simaruba*, *Leucaena glauca*, *Prosopis juliflora*, and *Guaiacum officinale* (Ewel and Whitmore 1973). These forests developed from agricultural lands that were primarily sugar cane or pasture as late as the 1930s (Thomlinson et al. 1996). Red mangrove areas were directly adjacent to the coast, lagoons, and major drainages and occurred in pure stands, whereas black and white mangrove formed mixed- and single-species stands inland from red mangrove areas. Dry forest sites were still further inland, adjacent to mangroves. Additional mangrove areas present at Roosevelt Roads Naval Station that were only rarely used by Northern Waterthrush included short-stature (<2 m) stands of black mangrove and stands of dead mangrove.

Study sites consisted of two dry-forest sites 1.5 km apart, two white mangrove sites 6.5 km apart, two black mangrove 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. Dry-forest sites did not have standing water. The dry season in this region lasts from January through April, when mean monthly precipitation is 7.5 cm or less (Daly et al. 2003). All mangrove sites had standing water, usually <1 m in January, but water depth gradually decreased as the dry season progressed toward April and May. Daily fluctuations in moisture levels infrequently occurred in coastal red mangrove areas during periods of exceptional tide fluctuations.

Bird sampling and radiotelemetry

Northern Waterthrush were captured at two-week intervals from late January to early April. We erected 10–15 12-m mist nets at each study site for a two-day period from 06:00 to 18:00. Waterthrush were captured without the use of playbacks or other enticements to avoid biases toward territorial or behaviorally dominant individuals. At the time of capture all individuals were banded with a unique combination of two colored leg bands and an aluminum U.S. Fish and Wildlife Service band. Each individual was measured (unflattened wing chord, tarsus length, and tail length to ± 0.5 mm), weighed to the nearest ± 0.1 g using a digital scale (Ohaus, Pine Brook, New Jersey, USA), and given a furcular fat score (categories: 0, none visible; 1, trace; 2, fat forming a solid sheet across the bottom of the furculum; and 3, fat filling furculum [Holmes et al. 1989]). Age was not determined due to the unreliability of aging methodology for this species during the winter period (Pyle 1997). A 75- μ L blood sample was taken for isotope analysis and to determine sex using a molecular technique (Griffiths et al. 1998). Previous studies have demonstrated that blood sampling does not affect mass of small passerines (Stangel 1986) or their survival (Hoysak and Weatherhead 1991). We sexed 270 birds in total (2002, $n = 153$; 2003, $n = 63$; 2004, $n = 54$).

We analyzed carbon isotopes in blood samples as a measure of habitat use (Marra et al. 1998) for all Northern Waterthrush radio tracked in 2003 and 2004 as well as a random sample of birds captured over the course of the study ($n = 229$). Radio-tracked birds served as a reference group with known habitat affiliations so that birds that were not tracked could be reliably assigned to a habitat category using discriminant function analysis. Habitat use could be inferred from these data because carbon isotope ratios in plant tissues are determined by both the water use efficiency and the photosynthetic pathways of plants (O'Leary 1981, Farquhar et al. 1989). Stable carbon isotope ratios are transferred up the food chain to invertebrates feeding on the plants and eventually to invertebrate predators such as the Northern Waterthrush (Peterson and Fry 1987). Because it reflects the spatial scale at which birds are feeding, isotope ratio can be used as an index of habitat moisture within and between habitats (Marra et al. 1998), with depleted $\delta^{13}\text{C}$ values being a signature of moist habitat and enriched values indicative of a drier habitat. We chose to use blood plasma since it has a quicker turnover rate than other blood components (2–3 days; Hobson and Clark 1993) and thus would best reflect the habitat that the bird was using just prior to the time of capture. All samples were collected within a two-week interval during January. Blood samples (≤ 75 μ L) were collected in capillary tubes via brachial venipuncture, placed on ice, and later (< 4 h) centrifuged at 1675.8 m/s^2 for 8 min to separate red blood cells from plasma. The blood components were separated using a Hamilton syringe and frozen at -15°C . We freeze-dried,

powdered, and loaded 1 mg of each sample into tin capsules for combustion (Hobson et al. 1997) in a continuous flow isotope ratio mass spectrophotometer (Europa Scientific, Cheshire, UK; University of California Davis, Stable Isotope Facility). Results of stable isotope analyses are expressed as the deviation (in parts per thousand) from the Pee Dee belemnite standard (Ehleringer and Osmond 1989).

From 2002 to 2004 we used radio transmitters attached to a subset of Northern Waterthrush to establish a reference group of stable carbon isotope samples from birds with known habitat affiliations. We radio tracked a total of 124 Northern Waterthrush over three seasons (2002, $n = 33$ females, 16 males; 2003, $n = 21$ males, 25 females; 2004, $n = 19$ males, 18 females).

Each individual was fitted with a radio transmitter that had a unique frequency ($n = 75$; Holohil BD2-A, Carp, Ontario, Canada; 0.74 g) using a leg harness technique (Rappole and Tipton 1991). Transmitter life ranged from three to four 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 to measure change in body mass and to replace failing transmitters with new units to extend the tracking period of these individuals. As a result, birds were tracked over a variable period ranging from 7 to 70 days (mean = 32.3, median = 26 days).

To quantify space use, one location per day of each individual was acquired during its tracking period. In 2002, individuals were found three times per day and little movement occurred within a day once a bird arrived on a feeding area from its roost site (within-day minimum convex polygon area = $0.07 \text{ ha} \pm 0.01$ [mean \pm SE], $n = 25$) thus little information was lost by finding birds once per day and we could increase our sample sizes of independent individuals. Location timing was varied randomly to reflect the full span of daylight hours, except for dawn (before 07:00) and dusk (after 17:00) periods when the majority of birds were commuting to distant roost sites (Smith et al. 2008). We used radio receivers (Fieldmaster 16, Advance Telemetry Systems, Isanti, Minnesota, USA) and three element Yagi antennas (Advanced Telemetry Systems) to relocate individuals with transmitters via homing. We approached as close as possible without disturbing the bird (to ~ 10 m). The observer location was then marked with a GPS (GPS 12, Garmin, Olathe, Kansas, USA), and the distance and bearing from this point to the bird were noted.

Home range moisture

We used satellite imagery to quantify wetness on radio-tracked Northern Waterthrush home ranges. A representative scene of 30-m resolution Landsat Enhanced Thematic Mapper (+ETM) imagery was used to quantify habitat conditions on 9 January 2001, which

corresponds to the time interval reflected in blood samples taken for isotope analysis of radio-tracked birds. Although the scene used does not correspond to a year during which fieldwork was conducted, habitat coverage within the study sites is identical (GIS data, Eagan, McAllister and Associates, *unpublished data*), and the scene used represents a year with typical annual rainfall patterns in which a pronounced dry season occurred between January and March following a much wetter period between September and December.

To derive an index of wetness from the Landsat scene, the tasseled cap transformation was performed using ENVI 4.3 (ITT Corporation 2006). This transformation uses a standard series of coefficients to create weighted sums of spectral bands that result 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). 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

Each time a bird was located, prey availability in the bird's foraging area was quantified using a timed, direct search of the ground substrate within two 0.25-m² quadrats (Johnson and Strong 2000). We placed the sample site as close as possible to the location without disturbing the bird. Each search was divided into a passive and active period. The first 3 min were spent visually searching the sample area and during the following 2 min the substrate (usually leaf litter) was overturned to expose hidden prey because the Northern Waterthrush is an active leaf-tosser during foraging (Schwartz 1964, Post 1978). All invertebrates encountered were classified by taxonomic order, and length was measured. Biomass was calculated using published length-mass regressions for Jamaican arthropods (Johnson and Strong 2000). Previous research using emetic sampling documented the winter diet of Northern Waterthrush in Panama at a similar coastal study site (Lefebvre et al. 1992, Poulin et al. 1994). We constrained our samples to arthropod orders and size classes that were a known component of waterthrush diets. Home range food availability was measured for 74 individuals, and samples taken per territory ranged from 5 to 36 (mean = 14, median = 12).

Statistical analyses

We used ANCOVA to examine variation in body mass during the day and across the span of the dry season. For this analysis, we excluded all birds with visible fat scores >1 (i.e., birds that had begun premigratory fattening) and entered a body size index variable (principal component 1 [PC1] from a principal components analysis [PCA] of wing, tail, and tarsus that explained 80.2% of variance) as a covariate. For birds captured multiple times within a season, we used only the first capture incident during a season, but considered captures of the same individual between years to be independent since the environmental conditions an individual experienced between years were independent. We added the following explanatory variables into an ANCOVA model for 229 Northern Waterthrush captures to examine their effects on body mass: body size, time of day, season, year, and habitat. The season component condensed banding periods into the early and late dry season. We also included habitat × time of day and habitat × season interactions to examine whether habitat affected mass change across these two temporal scales. All interactions including covariates were not significant and were removed from the final model. The habitat component was a binary variable representing the wet/dry dichotomy revealed by a discriminate function analysis of carbon isotopes using a single categorical habitat variable. The discriminant function was 93.5% accurate at assigning radio-tracked birds ($n = 78$) with known habitat affiliations to the correct category. We used the resulting classification coefficients to assign birds that were captured by mist nets that were not radio tracked to one of these habitat categories for subsequent analysis.

We used repeated-measures ANOVA to analyze rates of fattening of individual birds between habitats during the premigratory period. For this analysis, we constrained the data set to a one-month period spanning between mid-March and early April and divided the set into two sampling periods of equal length. Only individuals captured in both periods were included in the analysis. If they were captured more than once in a period, a mean fat score for that individual was used. Time of day was included as a covariate.

RESULTS

Satellite moisture patterns by habitat

The satellite wetness index produces a unitless measure of wetness with increasing values corresponding with increasing wetness. Radio-tracked Northern Waterthrush with home ranges in black mangrove (-51.80 ± 4.08 [mean \pm SE]; $n = 23$) and dry forest (-61.04 ± 3.41 ; $n = 30$) had significantly drier values than birds in white mangrove (-33.97 ± 4.54 ; $n = 17$) and red mangrove (-20.04 ± 5.00 ; $n = 14$; ANOVA with Tukey post hoc test, $F = 18.45$, $df = 3, 80$, $P < 0.0001$; Fig. 1).

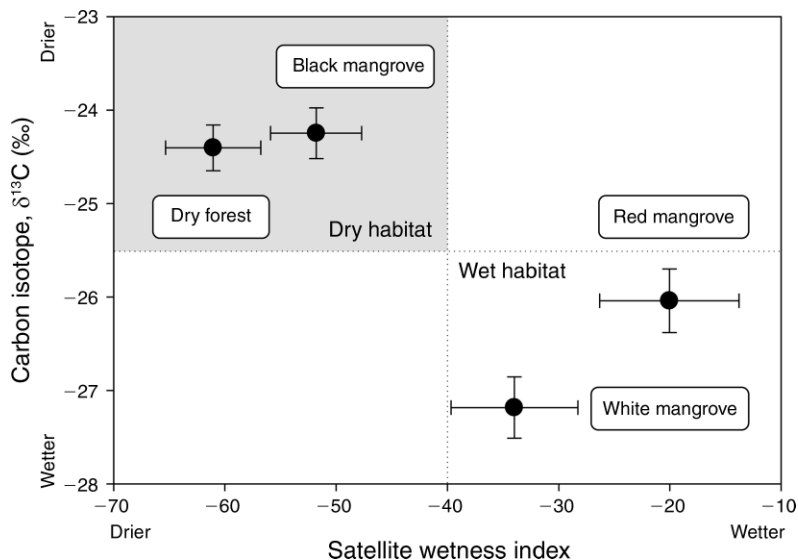


FIG. 1. Stable carbon isotope values (mean \pm SE) in blood plasma ($\delta^{13}\text{C}$) and mean tasseled cap wetness index values of home ranges for radio-marked Northern Waterthrush (*Seiurus noveboracensis*) in Puerto Rico. Results of stable isotope analyses are expressed as the deviation (in parts per thousand) from the Pee Dee belemnite standard (Ehleringer and Osmond 1989). See *Methods: Home range moisture* for an explanation of the wetness index. More negative stable isotope values represent wetter habitat conditions, whereas increasing wetness index values represent wetter habitat conditions. Birds occupying white mangrove (*Languncularia racemosa*) and red mangrove (*Rhizophora mangle*) showed significantly wetter values for both measures compared to birds using black mangrove and dry forest. The shaded section of the figure indicates the drier habitats.

Stable carbon isotopes as a measure of habitat moisture

Stable carbon isotope signatures from the blood of radio-tracked birds with known habitat affinities mirrored the moisture gradient found using satellite imagery (Fig. 1). Northern Waterthrush inhabiting black mangrove ($-24.25\% \pm 0.27\%$, $n = 22$; Fig. 1) and dry forest ($-24.40\% \pm 0.25\%$, $n = 27$) had significantly more enriched (i.e., drier) stable carbon isotope values (ANOVA with Tukey post hoc test, $F = 21.83$, $df = 3, 74$, $P < 0.0001$) compared to those occupying white ($-27.18\% \pm 0.33\%$, $n = 15$) and red mangrove ($-26.04\% \pm 0.34\%$, $n = 14$).

Habitat moisture and food availability

Northern Waterthrush home ranges in the dry habitats had significantly lower food availability (6.59 ± 0.78 g dry mass/ 0.25 m^2 , $n = 46$; Wilcoxon signed-rank test, $z = 3.52$, $P = 0.0004$) compared to the home ranges of birds occupying wet habitat (10.63 ± 0.93 g dry mass/ 0.25 m^2 , $n = 31$).

Seasonal mass change of radio-tracked birds and indices of moisture

We found a strong linear relationship between stable carbon isotope values in blood plasma and mass change of radio-tracked Northern Waterthrush over the dry season (adjusted $R^2 = 0.45$, $df = 1$, $P < 0.0001$, $n = 32$; Fig. 2A). Birds with more enriched stable carbon signatures, representing drier habitat conditions and lower food availability, lost body mass whereas birds with more depleted stable carbon isotope signatures

(wetter habitat conditions) gained mass as the season progressed.

The same pattern was evident when we examined the relationship between mass change and wetness of individual home ranges derived from satellite imagery (adjusted $R^2 = 0.27$, $df = 1$, $P = 0.0007$, $n = 35$; Fig. 2B). Once again birds occupying drier home ranges (represented by more negative values) tended to lose mass while those using wetter sites tended to gain mass as the dry season progressed.

Variation in habitat use and mass change by sex

For radio-tracked birds there was also a sex-specific pattern in mass change. An ANCOVA model ($F = 6.65$, $df = 3, 267$, $P = 0.0012$) including sex, the wet/dry habitat dichotomy, and a body size covariate (PC1 from a PCA of wing, tail, and tarsus) continued to show that birds in wet habitats had more positive trajectories of mass change ($F = 11.63$, $df = 1, 267$, $P = 0.0017$; wet least-squares mean mass change, 0.66 ± 0.15 g; dry least-squares mass change, 0.008 ± 0.12 g) but regardless of habitat type, males showed significantly better performance than females ($F = 6.65$, $df = 1, 267$, $P = 0.014$; male least-squares mass change, 0.66 ± 0.17 g; female least-squares mass change, 0.011 ± 0.15 g).

We found no evidence that sexes segregated by habitat. Based on a sample of 106 known-sex Northern Waterthrush, with habitat use inferred from carbon isotope results, sex ratio did not vary between the wet and dry habitat dichotomy ($\chi^2 = 0.202$, $P = 0.65$).

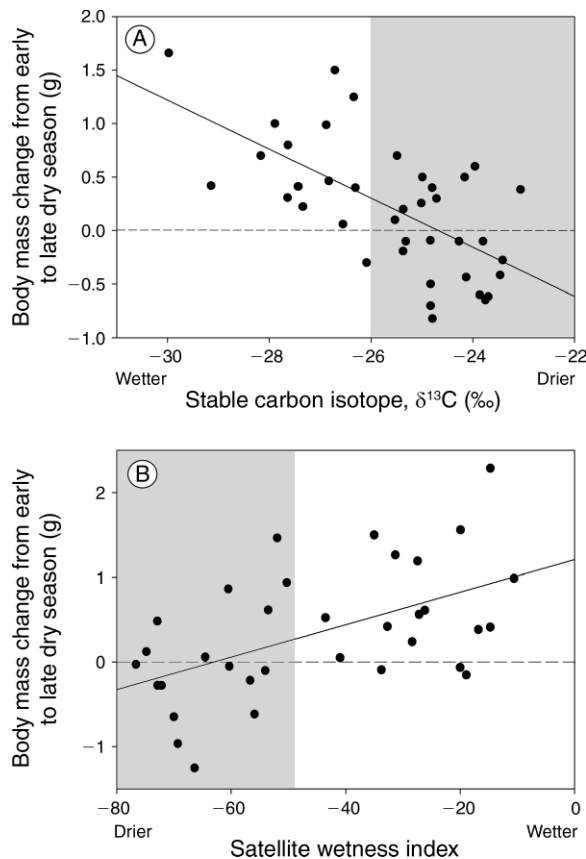


FIG. 2. (A) The relationship between stable carbon isotope values from blood plasma of Northern Waterthrush and change in body mass between the early and late dry season. (B) The relationship between satellite-derived wetness of Northern Waterthrush home ranges and change in body mass between the early and late dry season. The shaded sections of the plots indicate drier habitats identified using satellite imagery and stable carbon isotopes. See *Methods: Home range moisture* for an explanation of the wetness index.

Daily and seasonal mass change of birds that were not radio tracked

Nocturnal mass change.—Individual birds captured while moving between roosts and diurnal habitats (Smith et al. 2008) in the evening and recaptured again the following morning ($n = 29$) lost 7.6% of body mass on average (repeated-measures ANOVA, $F = 27.63$, $df = 1, 28$, $P < 0.0001$; evening mean, 16.2 ± 0.17 g; morning mean, 15.1 ± 0.16 g). We observed no significant difference in nocturnal mass loss of birds using wet vs. dry diurnal habitats ($F = 0.910$, $df = 2, 28$, $P = 0.35$; wet, $n = 17$, change, $-0.061\% \pm 0.011\%$; dry, $n = 12$, change, $-0.075\% \pm 0.013\%$).

Diurnal mass change.—An analysis (ANCOVA, Table 1) of body mass for single captures of Northern Waterthrush during the day ($n = 229$) revealed significant effects of body size, time of capture, year, and a significant habitat \times season interaction (Table 1). For the year effect, birds in 2003 (least-squares mean,

TABLE 1. Results from ANCOVA of factors predicting mass variation in the Northern Waterthrush (*Seiurus noveboracensis*) in Puerto Rico.

Source of variation	Sum of squares	df	F	P
Habitat (wet or dry)	3.99	1, 222	6.05	0.015
Body size	42.99	1, 222	65.15	<0.0001
Time of day (hour)	32.22	1, 222	51.85	<0.0001
Season (early or late)	1.30	1, 222	1.30	0.26
Year	20.87	2, 222	15.81	<0.0001
Habitat \times time of day	1.51	1, 222	2.29	0.13
Habitat \times season	7.39	1, 222	11.19	0.001

Notes: The dependent variable is Northern Waterthrush mass ($n = 229$); adjusted $R^2 = 0.41$. Habitat represents a dichotomy identified using carbon isotopes. Body size is principal component 1 of a principal components analysis of wing, tail, and tarsus length. Season represents the early (January–February) vs. late (March–April) dry season.

15.20 ± 0.114 g) were significantly lighter overall than birds from 2002 (least-squares mean, 15.63 ± 0.103 g) and 2004 (least-squares mean, 16.02 ± 0.092 g). The analysis also showed that Northern Waterthrush gained mass linearly throughout the day. The rate of gain was similar between habitats (wet habitats, 0.10 g/h, 95% CI, 0.048 – 0.147 ; dry habitats, 0.07 g/h, 95% CI, 0.057 – 0.083).

The habitat \times season interaction term revealed that differences in mass between wet and dry habitats became highly significant over the season (Fig. 3). At the beginning of the dry season, birds in both habitats had similar masses but by mid-March, at the peak of the dry season, body mass of birds occupying wet habitats had increased (early, least-squares mean, 15.48 ± 0.15 g; late, least-squares mean, 16.05 ± 0.13 g), whereas birds in dry habitats declined in mass during the progression of the season (early, least-squares mean, 15.60 ± 0.083 g; late, least-squares mean, 15.33 ± 0.12 g).

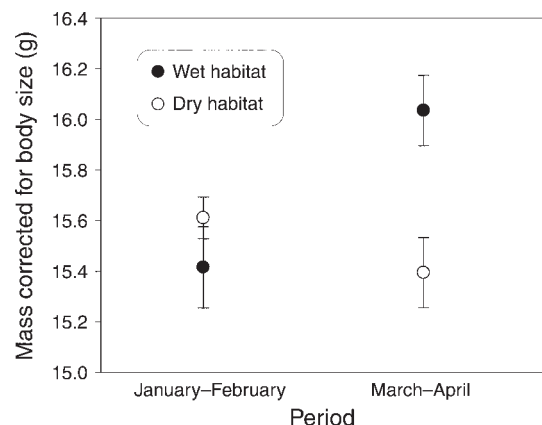


FIG. 3. Northern Waterthrush mass corrected for body size and time of day (least-squares mean \pm SE) as an estimate of physical condition during early (January–February) and late (March–April) dry-season periods.

Rates of fat deposition

Based on repeated captures of individuals, we found that rates of premigratory fat deposition just prior to spring migration to the breeding grounds from mid-March to early April varied by habitat. Northern Waterthrush using dry habitats ($n = 12$) significantly delayed fat deposition (repeated-measures ANOVA, $F = 23.26$, $df = 1, 11$, $P < 0.0001$; late-March mean fat score, 0.56 ± 0.20 ; early-April mean fat score, 1.21 ± 0.22) compared with those using wet habitats ($n = 25$; late-March mean fat score, 1.34 ± 0.17 ; early-April mean fat score, 2.15 ± 0.21).

DISCUSSION

Seasonal changes in moisture availability characterize tropical biomes throughout the world, and the manner in which animals, resident and migratory, respond and cope with such changes is poorly understood (Carson and Schnitzer 2008). Here, using radio tracking, along with stable carbon isotope and satellite wetness indices, we demonstrate that moisture determined food availability and consequent overwinter condition of a wet-habitat specialist, the Northern Waterthrush.

Our finding that males were significantly heavier than females regardless of habitat type provides evidence that there may be competition for high-quality home ranges. Males in both wet and dry habitats showed more positive rates of mass change over the course of the dry season when compared to females in the same habitat. This suggests that along the wet-dry continuum within these habitats, males may be securing higher quality home ranges. This is consistent with sex-specific patterns of spatial and social behavior we observed in a concurrent study (Smith 2008) in which we found that birds showing high levels of aggression (predominantly males) are more likely to be territorial and that birds maintaining territories occupied wetter sites with higher food availability than birds that used alternative space use strategies. The larger body size of males we observed may offer a competitive advantage in effort to secure and defend high-quality home ranges that could be limited in availability.

Overnight mass trajectories of Northern Waterthrush declined at equal rates and increased during the day, with a trend toward a slower rate of gain in drier habitats. Body mass loss overnight was on average 0.12 g/h, representing $\sim 7.6\%$ of total mass. This is similar to that observed for other small passerines (e.g., *Parus* spp., House Sparrow) wintering in temperate climates (Clark 1979, Lehtikoinen 1987) but to the best of our knowledge this is the first estimate of overnight mass loss for a Neotropical migrant on tropical nonbreeding grounds. That birds using both wet and dry habitats during the day experienced similar rates of overnight mass loss while using the same roosting habitat (Smith et al. 2008) suggests that the metabolic constraints of roosting are relatively constant regardless of diurnal habitat. Thus, the differences we detected in seasonal

mass change between wet and dry habitats are due to patterns of diurnal habitat occupancy and the food availability within each of those habitats.

Although we did not observe a significant difference in the rate of mass gain during the day between wet and dry habitats, the slope estimate of diurnal mass gain was less steep in dry habitats. The strong seasonal differences we observed in mass change suggest that each day presents a challenge to recover the mass lost during the previous evening. Even slight differences in rates of gain between habitats result in daily shortfalls in mass recovery that, over days and weeks, accumulate to become significant season-long declines in body mass, as we observed in Northern Waterthrush that occupied drier habitats. Habitat-specific differences in seasonal mass change have been reported for other Neotropical migrant species such as American Redstart (*Setophaga ruticilla*), Prairie Warbler (*Dendroica discolor*), Cape May Warbler (*Dendroica tigrina*), and Ovenbird (*Seiurus aurocapilla*) (Marra et al. 1998, Strong and Sherry 2000, Latta and Faaborg 2001, 2002, Studds and Marra 2005, Brown and Sherry 2006, Johnson et al. 2006), but ours is the first to link habitat moisture with habitat quality of home ranges to body condition at both daily and seasonal timescales.

We further found evidence that winter habitat occupancy may have influenced migration schedules of individuals. Rates of fattening differed significantly between wet and dry habitats, suggesting that before building fat reserves, birds in dry habitats first need to recover from season-long deficits of fat-free mass resulting from protein catabolism of muscle tissue. We did not document such a mechanism in this study but experimental results from several species of migratory passerines indicate that a disproportionate amount of protein mass loss under food-limited conditions is from digestive organs (Karasov et al. 2004). Smooth muscle mass of the digestive tract may need to be rebuilt before storage of fat reserves for migration progresses (Gannes 2002, Karasov et al. 2004, Pierce and McWilliams 2004). Delays in fattening likely contributed to a delayed departure and arrival on breeding areas and possibly to lower reproductive success, similar to what has been demonstrated in the American Redstart (Marra et al. 1998).

Rainfall and its impact on moisture availability to plants and resulting arthropod productivity varies annually (Dugger et al. 2004, Studds and Marra 2007). Since the Northern Waterthrush is an extreme-wet-habitat specialist, this species may be especially sensitive to even subtle deviations of annual precipitation and may be impacted heavily during El Niño/La Niña cycles (Giannini et al. 2000). Given that waterthrush forage primarily at the land-water edge, sites in anomalous years could be either too wet (i.e., under water) or too dry for optimal foraging. This could in part explain our result that birds in 2003 had significantly lower mass than the other two years of the study. Interestingly, 2003

corresponded with modest El Niño conditions, while 2002 and 2004 were normal years (NOAA, *available online*).⁴ This pattern may be evident because annual climate variation induces corresponding variation in the availability of high-quality habitats.

Of particular concern are predictions that levels of rainfall in the Caribbean basin will significantly decline over the next 50 years (Neelin et al. 2006, Rauscher et al. 2008). Such changes will have devastating effects on extant vegetative communities and their fauna. Our finding that a satellite-derived index of habitat moisture corresponds to an underlying gradient of habitat quality is a first step in developing tools to remotely map habitat quality over large areas and multiple time periods to make predictions about how changing conditions may affect populations. Such an advance would play an important role in our attempts to understand and predict how declining precipitation may affect this species and possibly others at broader spatial scales. Future research on climate change should emphasize not only how plant and animal species adapt to increasing temperature but also adapt to a drier future, especially in the Caribbean basin.

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⁴ www.elnino.noaa.gov

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