MULTIPLE SPACE-USE STRATEGIES AND THEIR DIVERGENT CONSEQUENCES IN A NONBREEDING MIGRATORY BIRD (*PARKESIA NOVEBORACENSIS*)

JOSEPH A. M. SMITH,[1,3] LEONARD R. REITSMA,[2] AND PETER P. MARRA[1]

[1]*Smithsonian Migratory Bird Center, National Zoological Park, Washington, D.C. 20008, USA; and*
[2]*Plymouth State University, Department of Biological Sciences, Plymouth, New Hampshire 03264, USA*

ABSTRACT.—We investigated the relationships among space-use patterns, home-range attributes, and individual characteristics to determine the consequences of different space-use strategies for the overwinter physical condition of Northern Waterthrushes (*Parkesia noveboracensis*). We have elsewhere demonstrated that heterogeneity in food availability drives the movement decisions of site-persistent and itinerant individuals during the nonbreeding period. Here, we show that intraspecific competition played an important role in determining where individuals initially and eventually settled. Territoriality, characterized by aggression, site-persistence, and exclusive home ranges, was more often found in males. Territorial birds gained mass over the winter, whereas birds that made midseason home-range shifts or that had home ranges with high intraspecific overlap tended to lose mass over the winter. The benefits associated with territoriality may be the result of maintaining higher-quality territories that were both wetter and had higher food availability than less exclusive home ranges. Our results suggest that despotism in the form of territoriality drives patterns of habitat occupancy, and in this system, high-quality habitat appears to be limiting for the Northern Waterthrush. This may have long-term consequences for the success of individual birds, because continued destruction of naturally limited habitats such as coastal mangroves, and predictions of a drying climate on wintering areas, have the potential to severely affect populations. *Received 17 October 2010, accepted 2 December 2010.*

Key words: aggression, habitat quality, nonbreeding season, Northern Waterthrush, *Parkesia noveboracensis*.

Estrategias Múltiples de Uso del Espacio y sus Consecuencias Divergentes en un Ave Migratoria No Reproductiva (*Parkesia noveboracensis*)

RESUMEN.—Investigamos las relaciones entre los patrones de uso del espacio, los atributos del ámbito de hogar y las características individuales para determinar las consecuencias de las diferentes estrategias de uso del espacio para la condición física invernal de *Parkesia noveboracensis.* En otra publicación hemos demostrado que la heterogeneidad en la disponibilidad de alimentos conduce las decisiones de movimiento de los individuos que persisten en un sitio y de los individuos itinerantes durante el período no reproductivo. Aquí, mostramos que la competencia intraespecífica jugó un rol importante en determinar dónde se establecieron inicialmente y eventualmente los individuos. La territorialidad, caracterizada por agresión, persistencia en el sitio y ámbitos de hogar exclusivos, fue encontrada más frecuentemente en los machos. Las aves territoriales subieron de peso durante el invierno, mientras que las aves que realizaron cambios en el ámbito de hogar a mediados de estación o que tuvieron ámbitos de hogar con una alta superposición intraespecífica tendieron a perder peso a lo largo del invierno. Los beneficios asociados con la territorialidad pueden ser el resultado de mantener territorios de mayor calidad que fueron más húmedos y tuvieron más disponibilidad de alimentos que los ámbitos de hogar menos exclusivos. Nuestros resultados sugieren que el despotismo, en la forma de territorialidad, conduce los patrones de ocupación del hábitat y en este sistema el hábitat de alta calidad parece estar limitado para *P. noveboracensis.* Esto puede tener consecuencias a largo plazo para el éxito de las aves individuales, debido a que la destrucción continua de los ambientes naturalmente escasos como los manglares costeros, y las predicciones de un clima más seco en las áreas de invernada, tienen el potencial de afectar severamente a las poblaciones.

THE DISTRIBUTION OF individuals within and among habitats has important implications for survival and reproduction (Brown 1969, Bernstein et al. 1991). Distribution patterns that result from intraspecific competition are often described using the theoretical models proposed by Fretwell and Lucas (Fretwell and Lucas 1970, Fretwell 1972). These include the ideal-free and the ideal-despotic distribution. In the ideal-free distribution, individuals are free to select any habitat patch without interference from other individuals and density is a function of habitat quality, so that all individuals have equal success regardless of the habitat they choose

(Godin and Keenleyside 1984, Walhström and Kjellander 1995). Conversely, with the ideal-despotic distribution, density is limited by competitive interactions (i.e., despotism), and less competitive individuals are excluded from high-quality habitats (Andrén 1990, Calsbeek and Sinervo 2002, Oro 2008).

Understanding which of these two models describe animals in the field is important because each model has distinct implications for the role of habitat availability in influencing population dynamics. If the ideal-free distribution underlies spacing patterns, then individual birds are not territorial, resources are not limited, and habitat availability is not likely to be a primary driver of population processes. If patterns consistent with the ideal-despotic distribution are revealed, this suggests that habitat is limiting and that through territoriality some individuals can secure a greater amount of resources than others (Marra et al. 1993, Holmes et al. 1996, Zimmerman et al. 2003). Furthermore, population processes can be greatly affected if excluded individuals are of a distinct age or sex class (Marra and Holmes 2001, Calsbeek and Sinervo 2002).

Territoriality in nonbreeding migratory songbirds is evidenced by aggression toward conspecifics, defense of small home ranges, and fidelity to a site both within and between years (Sherry and Holmes 1996). If territoriality occurs during the nonbreeding season, we would expect differential consequences for individuals across habitats and home ranges, with more competitive individuals maintaining better body condition than less competitive individuals (Sherry and Holmes 1996). Furthermore, we would expect that ecological determinants of fitness such as habitat quality would vary correspondingly, with more competitive individuals maintaining higher-quality territories (Sherry and Holmes 1996).

For nonbreeding migratory birds in the Neotropics, key ecological determinants are moisture (Janzen 1980, Lefebvre et al. 1994b, Parrish and Sherry 1994, Smith et al. 2010) and resulting food availability (Levings and Windsor 1984, Tauber et al. 1998, Strong and Sherry 2000, Brown and Sherry 2006). Throughout much of the nonbreeding range of migratory birds, a dry season sets in from December through mid-April, just prior to spring migration, which changes the distribution and availability of fruit, nectar, and invertebrate food resources (Janzen and Schoener 1968, Buskirk and Buskirk 1976, Tanaka and Tanaka 1982, Poulin et al. 1992). Such changes to habitats and their food resources may further intensify competition for high-quality sites that are often buffered from the effects of the dry season (Parrish and Sherry 1994). These changes may also lead less competitive individuals to disperse as habitat conditions deteriorate (Sherry and Holmes 1996).

We studied patterns of territoriality and overwinter site-persistence in a population of Northern Waterthrushes (*Parkesia noveboracensis*) that occupied a mosaic of nonbreeding habitats in Puerto Rico. Previous studies of territoriality in this species have led to different conclusions regarding patterns of winter space use. Schwartz (1964) showed Northern Waterthrushes to be site-faithful and territorial in a botanical garden, with agonistic behavior of color-marked birds at territorial boundaries described in detail. Conversely, mist-netting and resighting studies in Black Mangrove (*Avicennia germinans*) have reported overlapping home ranges and low within-season site fidelity (Lefebvre et al. 1992, 1994a, b; Lefebvre and Poulin 1996; Reitsma et al. 2002; Hunt et al. 2005). No studies have yet compared space use across multiple habitat types as a possible explanation for the conflicting results.

To that end, we examined evidence for defense of exclusive areas by individual Northern Waterthrushes by measuring aggression, estimating home-range overlap, and documenting overwinter site-persistence across multiple habitat types. We also examined whether a territorial space-use strategy resulted in the acquisition of higher-quality sites and tested whether this had consequences for the physical condition of individual birds by monitoring mass change over the late-winter dry season.

Methods

Study sites.—We conducted our research at the Roosevelt Roads Naval Station (18°20′N, 65°60′W) near Ceiba, on the east coast of Puerto Rico during January through April in 2003 and 2004. Our research was conducted 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, White Mangrove (*Laguncularia racemosa*), or Red Mangrove (*Rhizophora mangle*). Dry forest was a heterogeneous habitat with a more complex plant community (Smith et al. 2011).

Radiotelemetry.—Northern Waterthrushes were captured multiple times to measure condition and attach radio transmitters in late January, mid-February, early March, and early April. We erected 10 to 15 twelve-meter mist nets in each habitat type for a two-day period from 0800 to 1600 hours AST. The birds were captured without the use of playbacks or other enticements, to avoid biases toward territorial or behaviorally dominant individuals. For recapture attempts, additional netting efforts were targeted in individual home ranges. 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. Morphological measurements were taken on each individual (unflattened wing chord, tarsus length, and tail length to ±0.5 mm), and then all birds were weighed to the nearest ±0.1 g using an Ohaus digital scale. A 50-μL blood sample was taken to determine sex using polymerase chain reaction (Griffiths et al. 1998). Age was not determined because of the unreliability of ageing methodology for this species during the winter period (Pyle 1997). Only individuals captured ≥1 h after sunrise were used, to maximize the probability that they were using the habitat in which they were captured and not in commute from a roost location (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). In both years we deployed 30 transmitters in late January, 30 in mid-February, and 15 in early March.

To quantify space use, we acquired one location per day for each individual during its tracking period. We collected location data throughout the day to reflect the full span of daylight hours, except for dawn and dusk periods, when most of the birds were commuting to distant roost sites (Smith et al. 2008). We used radio receivers (Advance Telemetry Systems, Fieldmaster 16) and three-element Yagi antennas to relocate individuals with transmitters via homing. We approached as closely as possible without disturbing the bird (~10 m). The observer location was then marked with a GPS (Global Positioning System, Garmin GPS 12) and the distance and bearing from this point to the bird was noted.

On the basis of radiotelemetry observations, we defined overwinter site-persistence as the persistence of a bird in a single,

contiguous diurnal activity area. If a bird permanently moved from one activity area to another discrete location, this was considered a mid-winter home-range shift. Because the range of our transmitters was only ~100 m, such movements were evident when a bird simply was not detectable in its usual area (Smith et al. 2011).

Aggression.—We estimated conspecific aggression of birds with transmitters on diurnal home ranges by measuring their response to a 10-min chip vocalization playback (*n* = 47; Marra 2000). Results of previous studies with nonbreeding territorial migrants have shown that such presentations can reveal gradients in aggression that correspond to competitive ability and that often vary by sex and age class (Rappole and Warner 1980, Stutchbury 1994, Neudorf and Tarof 1998, Marra 2000). Presentations were made between 0900 and 1500 hours to ensure that the bird was on its diurnal activity area rather than moving to or from the roost (Smith et al. 2008). To make playback presentations, we located birds by homing with radiotelemetry to within 15 m and placed the speaker (Saul Mineroff Electronics, Model SME-AFS) on the ground, and the observer operated the playback from 5 m away. At the end of 10 min the response was classified as either positive (target bird vocalized and approached speaker to within 10 m or less) or negative (remained silent and held position or moved away from playback). Once we had calculated core home-range areas from radiotelemetry locations, any presentations made outside that core area were removed from analyses, to control for the possibility that birds may be more secretive at the edge of their home range (Bates 1992).

Home-range overlap.—Because we radiotracked individuals within a matrix of home ranges occupied by birds that were not radiotracked, we could not map all home ranges on the study site in order to estimate overlap. Instead, we developed a home-range overlap index. We did this by recording the locations of Northern Waterthrushes that were not radiomarked but that were observed in the vicinity of radiomarked birds and plotted these on home-range maps of radiotracked birds. To determine the location of unmarked birds, we conducted a 5-min point count of Northern Waterthrushes at each telemetry location. We recorded distance and bearing from the point count location to each detection. The majority (70%) of detections were within 25 m, and a distance sampling analysis in DISTANCE, version 6.0, revealed no habitat-level bias in detection probability. We then 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. 2006). We limited this analysis to birds that were tracked for at least 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). Once this area was established, we plotted the locations of Northern Waterthrushes detected during point counts at each telemetry location (mean [± SE] detections per home range = 16.6 ± 1.85; mean detections per survey = 0.9 ± 0.60). The proportion of point-count detections that fell within the core home range of a radiotracked bird was our index of overlap expressed as a percentage.

Body condition.—We determined mass change over the course of the dry season for birds that were captured with targeted mist netting in home ranges during both the early (January–February) and late dry season (March–April; *n* = 39). We used this measure of body condition because mass change during the nonbreeding season has been shown to be a strong predictor of annual survival for migratory birds (Johnson et al. 2006). Because Northern Waterthrush mass varies significantly by time of day (Smith et al. 2010b), we corrected for this by applying a standard coefficient to correct mass for time of day derived from a multiple regression analysis of 687 unique Northern Waterthrush captures across our study sites (Smith et al. 2010).

Habitat moisture.—We used a satellite-derived moisture index to assess habitat moisture on individual home ranges. The wetness component of the Tasseled Cap index provides a relative measure of 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). Pixel wetness values corresponding to each telemetry location were determined, to yield a mean wetness value for each home range in both January and March. The two resultant values provide an ecologically relevant measure of habitat wetness (Ranganathan et al. 2007) at the beginning and end of the dry season so that the effect of the dry season on habitat moisture can be estimated (Smith et al. 2011).

Arthropod biomass.—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 a 0.2-m² quadrat (Strong and Sherry 2000). Foraging areas in all habitat types were on the ground in leaf litter, mud, or mangrove pneumatophores. Each search was divided into a passive and an 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 length (mm) as measured in the field. Active and passive periods were combined for analysis. We calculated biomass using published length-weight 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 the 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). Home-range food availability was measured for 74 individuals, and the number of samples taken per home range ranged from 5 to 36 (mean = 14, median = 12).

Statistical analyses.—Chi-square contingency tables were used to examine relationships between categorical variables. Analysis of variance (ANOVA) was used to examine relationships between categorical predictors and continuous responses. The Kruskall-Wallis test was used in lieu of ANOVA in cases where data did not meet parametric assumptions. Home range-level analyses for wetness and food availability used mean values based on a sample of ≥15. All analyses were conducted using SPSS, version 15.0 (SPSS, Chicago, Illinois).

To examine the relationship between home-range exclusivity and change in body mass during the late nonbreeding period, we used classification and regression-tree analysis, or CART (Breiman et al. 1984). We chose CART analysis because preliminary data

screening revealed a nonlinear and heteroscedastic relationship that violated assumptions of standard regression (De'ath and Fabricius 2000). CART makes few assumptions about data properties and is effective at detecting change in mean and variance of response variables (De'ath and Fabricius 2000). We used tenfold cross-validation for each tree to determine the appropriate tree complexity (Breiman et al. 1984). Cross-validation consists of randomly partitioning data into 10 groups of approximately equal size, removing one set, and using the remaining sets to predict responses of the removed set. Estimated error for each subset is calculated and the tree with the number of nodes that has the lowest relative error is selected as the best model (Breiman et al. 1984). CART analyses were conducted using CART, version 6.0 (Salford Systems, San Diego, California). Statistics are reported as means ± SE.

RESULTS

Aggression.—Among the 47 experimental playbacks, 34% ($n = 16$) of the Northern Waterthrushes responded aggressively. Those that did not respond either moved away from the playback (23%; $n = 11$) or remained stationary and inconspicuous (42%; $n = 20$). In 20 of 31 cases in which the focal bird did not respond aggressively, an unbanded bird that was not the subject of the playback trial appeared and responded aggressively. The proportion of aggressive birds did not vary by habitat ($\chi^2 = 3.86$, df = 3, $P = 0.278$). Aggressive birds tended to have exclusive home ranges with significantly lower home-range overlap (mean = 14.2% ± 6.2 overlap; $n = 16$) compared to birds that did not respond aggressively (mean = 42.1 ± 4.7% overlap, $n = 28$; Wilcoxon ranked-sums $z = -3.35$, df = 1, $P < 0.001$; Fig. 1). Aggressive birds were also more site-persistent during tracking periods that ranged from 17 to 61 days ($\chi^2 = 5.01$, $n = 47$, $P = 0.025$). Nearly 90% of aggressive birds were site-persistent (87%; 14 of 16), whereas only 55% (17 of 31) of nonaggressive birds were site-persistent. Finally, a significantly greater proportion (Fig. 1; $\chi^2 = 5.62$, df = 1, $P = 0.017$) of aggressive birds
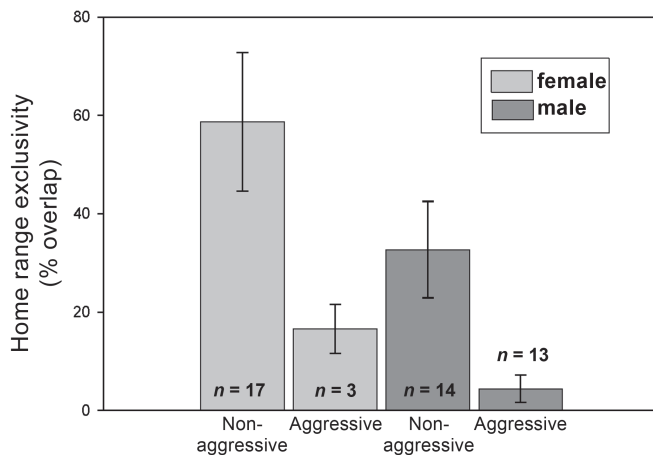
FIG. 1. The relationship between Northern Waterthrush aggression, exclusivity of their home ranges, and sex in birds overwintering near Ceiba, Puerto Rico, in 2003 and 2004. Aggressive birds had more exclusive home ranges (i.e., lower overlap) than nonaggressive birds, and a significantly greater proportion of aggressive birds were male.
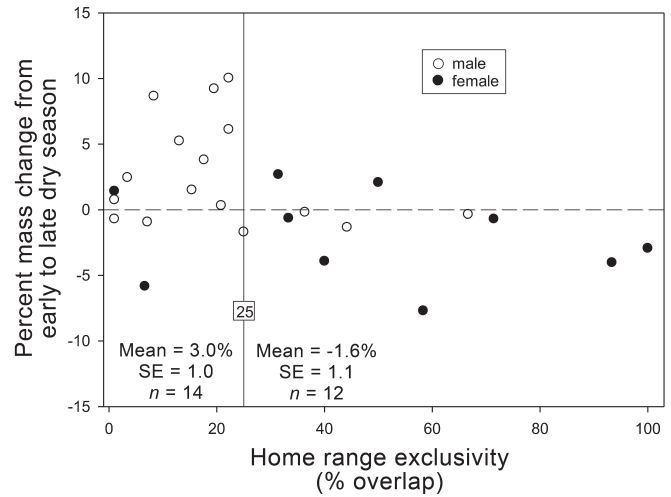
FIG. 2. Change (%) in body mass of Northern Waterthrush between January and March near Ceiba, Puerto Rico, in 2003 and 2004 in relation to the degree of home-range overlap. Results are from the CART analysis for the two-node tree size selected through cross-validation. The vertical dotted line indicates the home range overlap value (25%) that best explained variation in body mass change ($r^2 = 0.50$).

were male (81% of 18 birds) compared with nonaggressive birds (45% of 29 birds were male).

Home-range exclusivity.—Individual Northern Waterthrush with the most exclusive home ranges increased body mass from January to March whereas those with less exclusive home ranges experienced a decrease of body mass. Model cross-validation resulting from regression tree analysis of the relationship between home range exclusivity and over-winter mass change of birds revealed that a simple two-node model was the size that minimized relative error. This final model explained half of the observed variation in body mass change during the study period ($r^2 = 0.505$; Fig. 2). With two nodes in the model, this variation was partitioned at a single home-range overlap index value (25%). This value represents a threshold above which mass change remained stable or decreased as home-range overlap increased (mean = –1.9 ± 2.7%; $n = 16$), but below which body mass increased (mean = 4.3 ± 3.4%; $n = 22$).

Northern Waterthrushes with more exclusive home ranges also occupied higher-quality home ranges. Using the 25% exclusivity threshold to distinguish between presumptive low- and high-quality home ranges, more exclusive sites were wetter in January ($F = 8.49$, df = 1, $P = 0.006$; wetter values are more positive, low overlap mean wetness = –36.6 ± 3.96, $n = 21$; high overlap mean wetness = –53.2 ± 4.22, $n = 20$) and in March during the late dry season ($F = 8.64$, df = 1, $P = 0.005$; Fig. 3). More exclusive sites also had higher arthropod abundance (mean = 10.5 ± 1.16 mg dry weight 0.1 m^{-2}; $n = 23$) than sites occupied by birds with less exclusive home ranges (mean = 6.8 ± 1.27 mg dry weight 0.1 m^{-2}; Wilcoxon $z = -2.48$, $P = 0.013$; $n = 19$). We found no significant interaction between sex and home-range exclusivity with either wetness or food availability.

Patterns of space use.—We observed three patterns of space use: (1) site-persistent birds with low (<25%) home-range overlap
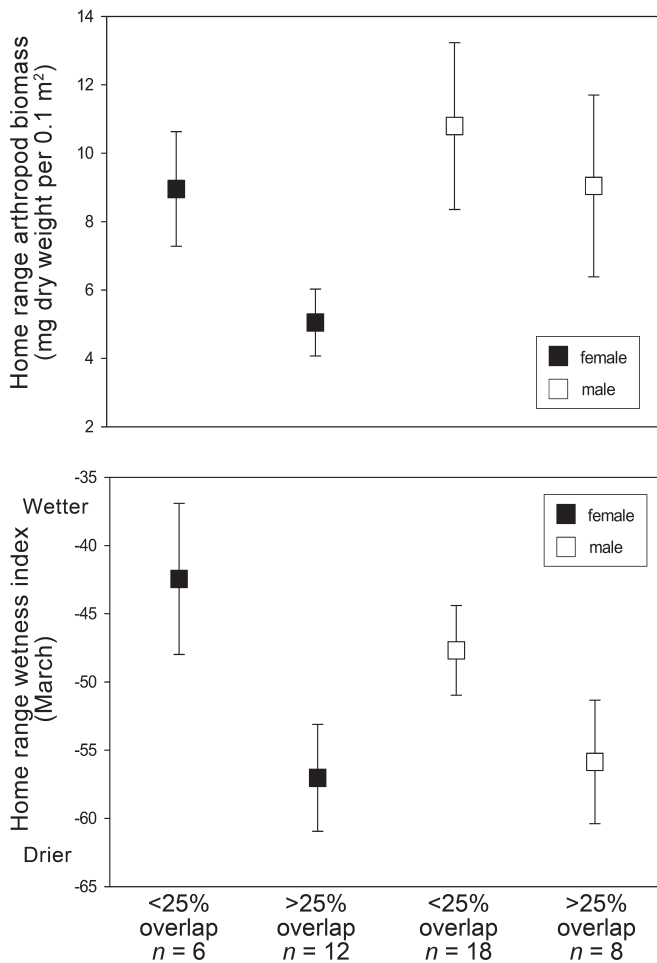
Fig. 3. Wetness and food availability on home ranges of territorial (<25% home-range overlap) and nonterritorial (≥25% overlap) male and female Northern Waterthrushes near Ceiba, Puerto Rico, in 2003 and 2004. More exclusive home ranges were wetter during the late dry season (lower frame). More exclusive sites also had higher arthropod abundance than the sites occupied by birds with less exclusive home ranges (upper frame).

(i.e., territorial); (2) site-persistent birds with high (<25%) home-range overlap; and (3) itinerant birds that made permanent shifts to new locations. Most birds were site-persistent between January and March (74.6% of 75 birds), and of those that were itinerant, most initially used either dry forest (48%) or Black Mangrove (44%). Only one individual each from White Mangrove (6%) and Red Mangrove (7%) dispersed. Thus, site-persistence differed depending on habitat ($\chi^2 = 15.83$, df $= 6$, $P = 0.007$).

Sex ratio also varied significantly across the three space-use categories ($\chi^2 = 7.4$, $P = 0.025$, $n = 44$). A greater proportion of territorial birds were male (80%; $n = 16$ of 20), compared with site-persistent, high-overlap (50% male; $n = 5$ of 10), and itinerant birds (31% male; $n = 5$ of 14). Post hoc chi-square pairwise tests across the three categories indicated that the comparison between territorial birds and site-persistent, high-overlap birds was not significant ($\chi^2 = 2.85$, $P = 0.091$, $n = 30$), but when territorial birds were

compared with itinerant birds, which were primarily female, the difference was highly significant (9 of 14 female; $\chi^2 = 6.9$, $P = 0.008$, $n = 34$). Sex ratio, however, did not vary significantly at the habitat level ($\chi^2 = 2.17$, $P = 0.54$).

Mass change differed significantly among the three space-use categories. Body mass of territorial birds increased over the dry season (mean $= 3.9 \pm 1.0\%$; $n = 12$), whereas body mass of site-persistent, high-overlap birds (mean $= -1.7 \pm 1.57\%$; $n = 5$) and itinerant birds (mean $= -1.6 \pm 1.17\%$; $n = 9$) tended to decline or remain stable. The difference between the latter two latter categories and territorial birds was significant (Tukey's post hoc comparison, $P < 0.05$). Seasonal changes in mass were also significant at the habitat level ($F = 4.10$, df $= 3$, $P = 0.014$, $n = 38$). Birds that initially occupied dry forest (mean $= -0.5 \pm 0.01\%$) and Black Mangrove ($0.6 \pm 1.48\%$) maintained mass, whereas those using red ($5.1 \pm 16\%$) and white ($3.6 \pm 1.24\%$) mangrove habitats gained mass (Tukey's post hoc test, $P < 0.05$).

Discussion

We have shown that Northern Waterthrushes exhibit multiple patterns of space use during the nonbreeding season. Most birds were territorial, and the areas used by territorial birds were wetter and had higher food availability than areas used by birds that employed alternative space-use strategies. Territoriality appeared to have clear advantages because these birds, on average, gained body mass over winter whereas birds that used alternate strategies maintained or lost mass.

Overwinter site-persistence was most likely determined by levels of home-range food availability (Smith et al. 2011). Here, we have shown that birds that shifted their home ranges during late winter also experienced a decline in body condition, which suggests that this behavior was not simply an alternative space-use strategy equivalent in outcome to territoriality. Midseason movements may represent attempts to locate better foraging conditions as birds depart from areas that are (or become) suboptimal. The disparities among birds employing different space-use strategies suggest that habitats used by Northern Waterthrushes vary in quality and that there is competition for high-quality winter sites.

Habitat limitation is of particular importance if competitive ability depends on sex or age class (Marra and Holmes 2001, Catry et al. 2004). Males were more aggressive and more likely to be territorial than females. Although this species is monomorphic with respect to plumage, males are significantly larger than females (J. A. M. Smith unpubl. data). Thus, males appear to have a competitive advantage that results in a higher probability of acquiring high-quality sites. The resulting sex-specific difference in body condition may have important demographic consequences for females, such as decreased survival (Studds and Marra 2005) and delayed migration departure schedules (Marra et al. 1998, Smith et al. 2010) that could subsequently result in lower breeding success (Norris et al. 2004).

Our findings indicate that the space-use patterns of Northern Waterthrushes are consistent with the ideal-despotic distribution rather than the ideal-free distribution. As predicted by the ideal-despotic model, we observed that more competitive individuals, which were more aggressive and territorial, acquired higher-quality home ranges and were in better body condition than

less aggressive individuals. Previous studies that concluded that Northern Waterthrushes were not territorial described patterns of low-overwinter site fidelity similar to that which we observed in Black Mangrove and dry forest (Lefebvre et al. 1994a, Reitsma et al. 2002). Schwartz (1964), on the other hand, showed that Northern Waterthrushes were territorial in an irrigated botanical garden. Our work reconciles these disparate findings by documenting a continuum of space-use strategies that is dependent on competitive ability and habitat selection. It is likely that in high-quality, seasonally stable habitats, territoriality is more common whereas in lower-quality or seasonally dynamic habitats, alternative strategies are more prevalent.

It has been hypothesized that alternative patterns of space use, such as midwinter dispersal and floating in an otherwise territorial spacing system, result in lower fitness (Brown 1969, Fretwell 1972). Our results are among the first to document this in a Neotropical migratory bird and confirm that alternative strategies are employed by less competitive individuals that occupy suboptimal habitats. The presence of such individuals in this study system provides further support for the hypothesis that winter habitat is limiting.

Precipitation records reveal a significant drying trend in the Caribbean over the past 50 years (Neelin et al. 2006). Climate-change models for the Caribbean, a region that comprises a significant portion of the nonbreeding range of the Northern Waterthrush, predict that this drying trend will continue (Neelin et al. 2006). The loss of mangrove habitat as a result of climate-change-induced sea-level rise will further affect the habitats used by this species (Parkinson et al. 1994, Gilman et al. 2007). These predictions suggest that the availability of high-quality habitats (mangroves) may decline and that low-quality habitats (dry forest) could decline further in suitability for migratory birds. The main question in this system is whether changes in nonbreeding habitat availability and quality will affect population processes in subsequent parts of the annual cycle (Runge and Marra 2005). Such information is essential for understanding songbird population dynamics and for applying sound conservation strategies in a changing world.

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