

SITE FIDELITY AND EPHEMERAL HABITAT OCCUPANCY: NORTHERN WATERTHRUSH USE OF PUERTO RICAN BLACK MANGROVES DURING THE NONBREEDING SEASON

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ABSTRACT.—We studied the dispersion of Northern Waterthrushes (*Seiurus novaboracensis*) in southwestern Puerto Rico during four nonbreeding seasons, 1996–1999. Densities were high (up to 13 birds/ha) on a 3-ha mature black mangrove (*Avicennia germinans*) study plot, but were significantly lower during periods of high water levels. Individuals exhibited site fidelity within and between seasons. Feeding areas were small (mean = 0.074 ha \pm 0.041 SD) and there was considerable overlap tolerated among conspecifics. Waterthrush density decreased when water submerged their primary foraging substrate: woody debris and pneumatophores. Inter-annual returns were similar to other Neotropical migrants (mean = 50%) but site persistence was low due to periodic flooding. In September 1998, hurricane Georges flooded the plot and blew down >90% of the black mangrove trees. This drastic habitat alteration was followed by a drastic decline in waterthrushes using the study area. Individuals left feeding areas for overnight roost sites in red mangroves (*Rhizophora mangle*). This latter finding, coupled with site fidelity and high return rates concurrent with low site persistence, suggests that waterthrushes exhibit high plasticity in their use of habitat during the nonbreeding season, but may rely upon mangroves for overwinter survival. Received 15 May 2001, accepted 13 March 2002.

Nearctic-Neotropical migratory passerines spend over half of each year in the tropics, commonly returning to the same sites (Faaborg and Arendt 1984, Lynch et al. 1985, Kricher and Davis 1986, Holmes et al. 1989, Winker et al. 1990). This realization has likely influenced the increase in studies that focus on winter habitat loss and its effect on populations of migrants. While almost all migrants are territorial during the breeding season, winter habitat use varies widely between species and many species' use of habitat is still poorly understood. Population studies recently have demonstrated that optimal nonbreeding habitat may be limiting, at least for some species (Rappole et al. 1989, Marra et al. 1998), thus the high rate of deforestation in Middle America and the Caribbean potentially will have a great impact on migrant bird populations (Rappole and Powell 1986, Wunderle and

Waide 1994). Already, forest cover is estimated to have declined to about 21% of island land area in the Caribbean (Wunderle and Waide 1994).

Mangrove forests have some of the highest abundances of overwintering migrants in the Caribbean (Arendt 1992, Lefebvre et al. 1992, Robbins et al. 1992, Sliwa and Sherry 1992, Wunderle and Waide 1993). However, few detailed population studies have been conducted in mangroves (but see Holmes and Sherry 1992; Lefebvre et al. 1992, 1994; Lefebvre and Poulin 1996; Marra and Holmes 2001). Several studies have used marked individuals on the wintering grounds to quantify overwinter site persistence, annual return rates, and dispersion (Winker et al. 1990, Holmes and Sherry 1992, Mabey and Morton 1992, Stai- cer 1992, Wunderle 1992, Marra et al. 1998). Some migrants in mangroves defend territories (Holmes et al. 1989, Rappole et al. 1989, Mabey and Morton 1992).

The Northern Waterthrush (*Seiurus novaboracensis*) has been documented as the most abundant migrant passerine in some mangroves (Lefebvre et al. 1992, Wunderle and Waide 1993). Lefebvre et al. (1994) and Lefebvre and Poulin (1996) concluded this species was not territorial in either Venezuelan or Panamanian mangroves, respectively, in contrast to Schwartz's (1964) reports of territori-

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ality in this species within an irrigated botanical garden in Venezuela.

We monitored the use of a mature black mangrove (*Avicennia germinans*) forest by a marked population of Northern Waterthrushes over four nonbreeding seasons to determine whether this species (1) exhibits site fidelity in this habitat, and (2) responds to changes in habitat suitability within and between seasons. Natural changes that occurred during our study allowed us to document the degree of plasticity that this species exhibits in response to both short term and long term habitat changes.

STUDY AREA AND METHODS

We mapped the spacing pattern, and measured density and site persistence of Northern Waterthrushes on a 3-ha plot within a mature black mangrove forest. This site (18° 01' N, 67° 10' W) was located on the Boqueron Bird Refuge, a 182-ha reserve located 8 km south of Cabo Rojo in southwestern Puerto Rico and managed by the Puerto Rican Dept. of Natural Resources. This forest was separated from a red mangrove (*Rizophora mangle*) stand and open lagoons by a manmade dike. The plot had a mean canopy height of 12 m and a mean of 256 trees/ha, nearly all of which were black mangroves. The forest floor was a combination of shallow water (<25% cover when not flooded), leaf litter, mangrove pneumatophores, and woody debris. Waterthrushes foraged predominantly on the forest floor, but also searched for food on woody debris, upturned root masses, and in black mangrove trees.

Periodic flooding of the plot occurred throughout our study as a result of variations in rainfall between September and December. We measured water depth beginning in January 1997 using a gauge placed in a channel adjacent to the plot and calibrated the channel depth to the plot water depth. For time periods prior to the placement of the gauge in the field, we estimated the water levels by comparing the relative exposure of pneumatophores and percent open water cover on the plot. March 1997 and 1998 and January 1998 were similar in water level to the conditions prior to installing the gauge, and measurements during these three intervals allowed reasonably accurate estimates of the two periods previous to installation. Before Hurricane Georges, the mangrove forest had a closed canopy and little foliage below 2.5 m. The hurricane dramatically altered this habitat in September 1998, leaving <10% of the trees standing. The plot was still flooded 6 months after the hurricane, and little vegetative regrowth had occurred. We estimated the water levels for the periods after the hurricane by comparing the height of water on prominent standing trees and other unaltered features on and around the plot to flooded periods when the gauge was in place, such as January and October 1997.

We collected data in January during the 1995–1996 nonbreeding season (September through early April), and in October, January, and March for the following 3 years. We captured Northern Waterthrushes in mist nets, and color banded each bird. We measured weight, fat (0–4 visual index of interfurcular fat), and unflattened wing chord. During the last 2 years, we collected 5 μ l of blood from the brachial vein of birds to sex individuals of this monochromatic species. We used a combination of PCR and electrophoretic detection of diagnostic protein bands to determine sex (Griffiths et al. 1996) for some individuals, and nonoverlapping wing chord length distinctions in others (>78 mm for males, <71 mm for females; Pyle et al. 1987).

We systematically searched the plot for Northern Waterthrushes during each time period, and locations and movements of banded and unbanded birds were recorded. A bird was considered a resident if it was relocated ≥ 4 days in the same area in one time period of a single season. All observations were compiled during each trip to produce minimum activity ranges, which were the minimum convex polygons encompassing all observations of individual birds (Holmes et al. 1989). We refer to these minimum activity ranges as feeding areas rather than territories because individuals did not aggressively exclude conspecifics, but they did exhibit within and between season site fidelity, and they actively fed in these restricted areas. Interannual return rates and site persistence were based upon resightings and recaptures. We investigated movement of birds toward and away from the plot using mist netting during all three times of the nonbreeding season. An 80–120 m mist net lane was operated for 4 h after dawn and 4 h preceding dusk on the dike along the west edge of the plot. Travel direction was recorded for each bird captured.

We used simple regression to correlate water depth on the plot with bird density, and to correlate density with the amount of overlap in feeding areas. Overlap was quantified as the percent cover of the plot in which two or more feeding areas overlapped. We used chi square analysis to test for differences in travel direction of birds into the mist net lane after dawn compared to before dusk. Seasonal changes in body mass/wing chord ratios were analyzed using ANOVA to measure weight loss during the nonbreeding season. To obtain an adequate sample size for analysis of all three time periods of each season, the sample included all Northern Waterthrushes caught on the plot and on the dike adjacent to the plot, most of which did not have feeding areas on the plot. We also used a *t*-test to analyze differences in body mass/wing chord ratios for resident birds on the plot during October and January, for which we had adequate sample sizes.

RESULTS

The number of Northern Waterthrushes on the 3-ha study plot ranged from 39 in October 1996 to 0 in March 1999 (Fig. 1). Feeding areas were small (mean = 0.074 ha \pm 0.041

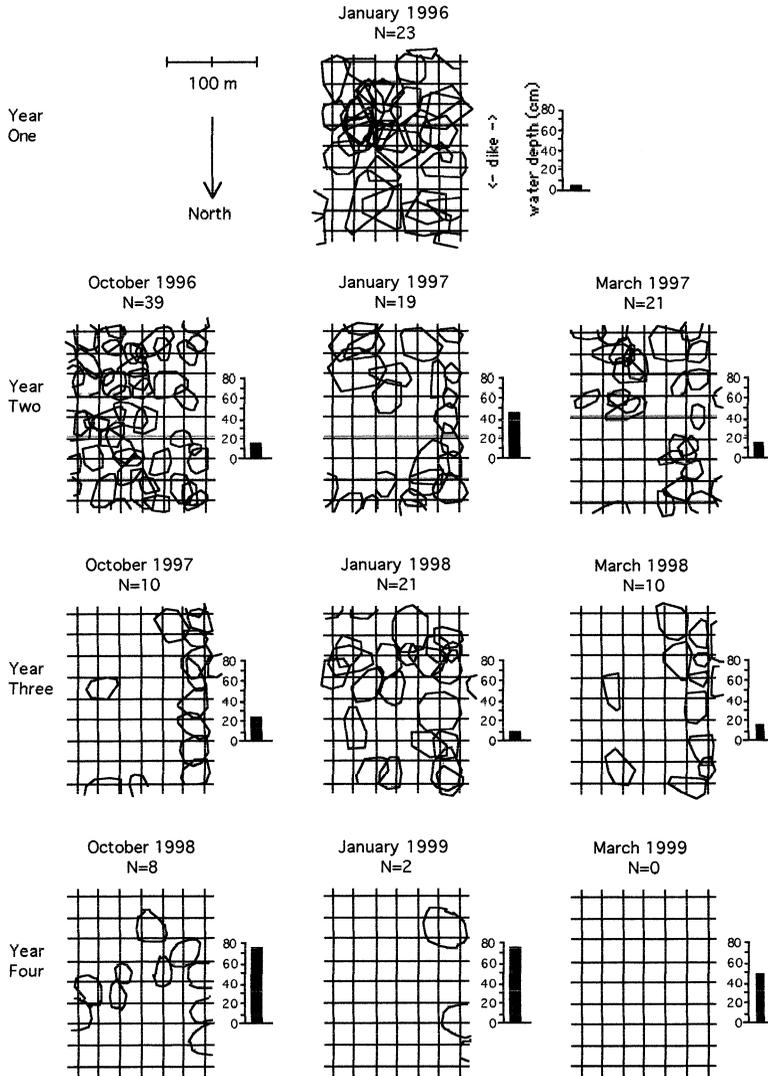


FIG. 1. Feeding areas of Northern Waterthrushes on a 3-ha mature black mangrove study plot at the Boqueron Bird Refuge in southwestern Puerto Rico during four nonbreeding seasons. Each polygon encloses all the observations of individually color-marked birds that were resighted ≥ 4 times on the plot during each designated time period. The number of mapped birds and the mean water depth of the plot (WD, in cm) is shown. The entire plot is covered with water when WD > 25 cm. The west side of the plot is bounded by a dike. Hurricane Georges drastically altered the structure of this forest plot in September 1998 just prior to Year Four. By March 1999, no resident birds remained.

SD, $n = 158$). During times of high density, there was greater overlap in feeding areas ($F_{1,8} = 26.49$, $P = 0.0009$, $r^2 = 0.768$). Density fluctuated widely within and between seasons and was negatively correlated with water depth ($F_{1,7} = 5.403$, $P = 0.049$, $r^2 = 0.403$). Flooding occurred between October 1996 and

January 1997 with a corresponding $>50\%$ decline in density (Fig. 1). Flooding also occurred prior to October 1997 and October 1998 and was associated with much lower densities compared to October 1996. The lowest densities occurred after severe hurricane damage (October, January, and March of the

fourth season). Overall site persistence was low (42%) and varied from one interval to another.

Of 23 Northern Waterthrushes with well-documented feeding areas on the plot during January of 1996, 12 (52%) returned the following season and five (22%) returned again the next season. Return rates were lower between the second and third seasons of this study (8 of 26 birds, 31%) and lower still between the third and fourth seasons (2 of 14 birds, 14%). Of 63 well-mapped birds over the 4-year study, 21 (33% of the original cohort) had feeding areas in ≥ 2 consecutive years and five (7.9% of the original cohort) had feeding areas in three consecutive years. One of the 3-year occupants was recaptured the fourth season but did not have a known feeding area on the plot.

Waterthrushes lost mass throughout the season. The body mass/wing chord ratio of all waterthrushes, including transients, decreased throughout the nonbreeding season from October (mean = 0.23 g/mm \pm 0.02 SD, n = 158) to January (0.22 \pm 0.01 SD, n = 102) and then further in March (0.21 \pm 0.02 SD, n = 9; $F_{2,226}$ = 4.71, P = 0.01). For resident birds, we had adequate sample sizes to compare only October to January, and the pattern was consistent (October mean = 0.23 \pm 0.02 SD, n = 23, and January mean = 0.22 \pm 0.02 SD, n = 47; t = 1.998, df = 68, P = 0.05).

Birds consistently moved across the dike from the red mangrove side in the morning and from the black mangrove side at dusk (n = 100, χ^2 = 37.37, df = 1, P < 0.001). Of the birds captured in the morning, 64% (n = 45) were going from red to black mangrove. Of the birds captured in the evening, 89% (n = 55) were going from black to red mangrove.

We determined the sex of 25 resident birds, 10 using blood DNA and 15 using wing chord lengths. Genetic analysis of blood showed no sex bias (6 of 10 sexed were males). The majority (14 of 15, 93%) of all birds sexed by wing chord length were females. Therefore, 7 of 25 birds of known gender with well-mapped feeding areas on the plot were male (28%). The sample sizes were too small to compare sex ratios within or between seasons. An additional 45 transients caught on or adjacent to the plot were sexed using blood

DNA and 13 were males (28.9%), a proportion consistent with that of the residents.

DISCUSSION

When not flooded, this mature black mangrove forest had among the highest density (13 birds/ha) of marked resident birds of any previously recorded Neotropical migrant population (but see Marra and Holmes 2001, who reported 15 American Redstarts, *Setophaga ruticilla*, per ha during fall and 12/ha during spring). However, the conditions of this and other habitats (PH unpubl. data) used by Northern Waterthrushes were not stable. On the black mangrove plot, densities were inversely associated with water level. A similar pattern was documented in other habitats in southwestern Puerto Rico (LR unpubl. data). Moist ground appears to be the most suitable feeding substrate for waterthrushes in black mangroves, but standing water that submerges pneumatophore tips precludes their ability to forage on the ground. Woody debris and dead trunks remain useable when pneumatophores are submerged, but the majority of waterthrushes we observed foraging were walking on the ground among the pneumatophores. The linear dispersion of individuals along the drier dike during periods of flooding (Fig. 1: October 1997 and March 1998) provides further evidence for the importance of water level. These individuals had moist ground substrate for foraging, allowing them to persist along the edge of the plot.

The response of Northern Waterthrushes to Hurricane Georges was marked. The hurricane covered the plot with an estimated mean of 0.75 m of water and destroyed most of the canopy trees. Even though many birds were caught in nets on the dike and on the plot within 3 weeks after the hurricane, these birds likely were spending most of their time off the plot because only 2 of 48 caught on or near the plot were resighted. Bird activity on the plot declined during the 2 weeks following the hurricane, October 6–22, 1998, and was markedly lower still in January and March 1999. This probably was due to a lack of preferred foraging substrate because of the flooding and the disappearance of the canopy, which provided shade (see Schwartz 1964 for proposed minimum habitat requirements).

The fact that abundance on the plot varied

so greatly during each winter (19 to 39, 10 to 21, and 0 to 8) demonstrates the ability, and perhaps the necessity of waterthrushes to shift their daytime feeding areas. Although most of these birds were found repeatedly on one small part of the plot while they were residents, they went elsewhere when water covered the foraging substrate and they presumably found suitable habitat elsewhere. Individuals banded during October sometimes were not present during January, but were seen on the plot in March, indicating that the disappearance of birds from the plot during high water did not represent mortality but movement to other areas. This is consistent with the lack of season-long residence by waterthrushes in Panamanian mangroves (Lefebvre and Poulin 1996). In Panama, waterthrushes appeared to be tracking food abundance, and the authors suggested that the movement they documented may represent a broader pattern of midwinter migration for at least some species of Neotropical migrants. The large number of transient birds captured on or near the plot and never resighted suggests that many individuals simply moved through the plot. Recent evidence from telemetry suggests that many "transients" move considerable distances through many habitat types en route from regular feeding areas to roost sites (LR unpubl. data).

Although many species of Neotropical migrants are territorial during the nonbreeding season (Lynch *et al.* 1985, Holmes *et al.* 1989, Rappole *et al.* 1989, Marra *et al.* 1998), Northern Waterthrushes are not when they occupy mangroves (see also Lefebvre *et al.* 1994 and Lefebvre and Poulin 1996). Two to five individual feeding areas often overlapped, and overlap increased significantly with increasing density on the plot. Two to three individuals occasionally were observed <2 m from each other, and when flushed they often would fly in the same direction. Some individuals did, however, exhibit site fidelity to feeding areas, returning to the same specific areas on the plot on successive days and in successive years. Return rates were highest from first to second year (52%), and the lower rates in subsequent years may have been influenced by the higher incidence of flooding from 1997 through 1998. Schwartz (1964) documented classic territorial behavior during the second half of

the nonbreeding season among a local population of Northern Waterthrushes within an urban park in Venezuela, but this territorial defense may have been in response to artificial ground moisture supplied by irrigation. Although most wintering migrants are territorial or occur in mixed species flocks, species with overlapping home ranges have been reported elsewhere in Puerto Rico (Staicer 1992).

The consistent predictable movement of individuals from black to red mangrove for overnight roosting was further supported by a minimal amount of radio telemetry (LR unpubl. data). Individuals that fed in the black mangroves traveled to the red mangroves across the dike in the evening and then back to the black mangroves the next morning. This use of red mangroves was further corroborated by more detailed studies at a site 6 km to the south and a site on the east side of Puerto Rico (LR unpubl. data).

Body mass to wing chord ratios declined throughout the nonbreeding season from October to March. This analysis was consistent for resident birds and for residents and transients combined. The pattern is similar to that which occurred in American Redstarts in Jamaica (Marra *et al.* 1998) and Belize (S. Baird unpubl. data). Body condition might be expected to decline given the general drying trend in most of Puerto Rico, and especially in the southwest, from January to the end of March, which often reduces arthropod abundance.

Individuals of both sexes had feeding areas on the plot. Birds that moved through the plot and those that remained on it to feed both showed similar sex ratios of three females to one male. Despite the fact that the majority (70%) of captured birds were not sexed and therefore the complete demographic makeup of this population was not known, our data suggest that waterthrushes do not appear to sexually segregate by habitat, at least to the same degree as some other migrant warblers such as the American Redstart (Marra and Holmes 2001, Parrish and Sherry 1994). We conclude that both sexes were residents on the plot for the duration of our monitoring, but we do not know the precise sex ratio at any single interval of our study.

The high density of Northern Waterthrushes documented in black mangroves in this study

and others (e.g., Lefebvre et al. 1994) indicates the importance of this habitat to sustaining waterthrush populations during the non-breeding season. This habitat is subject to considerable short term change, mostly due to changes in water levels, but also due to changes in food abundance (Lefebvre and Poulin 1996). This might particularly influence its suitability for a ground forager such as the Northern Waterthrush. As a result, Northern Waterthrushes must be capable of changing locations over the course of any single non-breeding season, and other locations and habitats may be essential to their survival. Lefebvre and Poulin (1996) suggest that migrant dwellers of mangroves may regularly migrate into and out of habitat patches, tracking the phenology of arthropod food in each. In our study, the changes in habitat quality resulting from flooding also may eliminate the benefits of territorial behavior in favor of more opportunistic occupation of suitable feeding sites.

Despite the documented within season mobility of this species, the high densities in mangroves, the return to mangroves when this habitat becomes suitable, and the daily movement back into red mangroves to roost, all underscore the importance of mangrove habitats to Northern Waterthrushes. The rapid human destruction of mangroves has the potential to cause declines in the species' population.

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