

HABITAT USE OF THE LOUISIANA WATERTHRUSH DURING THE NON-BREEDING SEASON IN PUERTO RICO

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ABSTRACT.—We used radiotelemetry to quantify habitat and spatial use patterns of neighboring Louisiana Waterthrush (*Parkesia motacilla*) along two streams in the Caribbean National Forest in Puerto Rico during 2005–2007. Home range sizes varied with younger birds having larger home ranges and core areas than older birds. All birds occupied some length of stream but a wide range of off-stream habitats were also used. Off-stream habitats included a range of disturbance from residential areas to small saturated pastures. Neighbors exhibited a wide range of overlap in home ranges ($\bar{X} = 20\%$) and older birds had more overlap than younger birds. The greatest percent of foraging time was along streams (64.4%) followed by muddy substrate (26.5%), housing developments (7.4%), and roads (1.7%). The greater proportion of time foraging along streams indicates this is the preferred habitat for this species. Use of off-stream habitat indicates a strategy of exploiting food-rich ground substrates, and in particular those with high moisture. Received 28 September 2010. Accepted 5 February 2011.

Identifying mechanisms that limit and regulate populations is critical in understanding population dynamics. Identifying these mechanisms for migratory animals is difficult because of the large and often separate geographic areas in which they occur annually (Marra and Holmes 2001). Multiple processes can operate at different times in the annual cycle and in geographically distinct locations. These processes can influence factors that affect population growth rate (i.e., survival and reproduction) including inter- and intra-specific competition, and predation. Most studies of long-distance migratory birds have focused on population regulating mechanisms during the breeding season.

The primary resource requirements for migratory birds during the non-breeding season are food and shelter from predators (Brown and Sherry 2008). Food availability (Sherry and Holmes 1996, Sherry et al. 2005), dominance-mediated habitat segregation (Wunderle 1992, Parrish and Sherry 1994, Marra and Holmes 2001), predator pressure (Watts 1991), and proximity to breeding areas (Cristol et al. 1999, Jenkins and Cristol 2002) affect the distribution of many neotropical migrants during the non-breeding season.

Habitat occupancy during the non-breeding season is an important component of the annual cycle for neotropical migratory birds (Marra et al. 1998); however, empirical data on habitat occu-

pancy and use during the non-breeding season are lacking for most neotropical migrants. Non-breeding occupancy has been shown to affect annual survival (Marra and Holmes 2001), spring migration departure dates, arrival in breeding areas, number of young produced (Reudink et al. 2009), and natal dispersal (Studds et al. 2008).

Neotropical migrants use multiple behavioral strategies including territoriality (Holmes and Sherry 1992, Marra et al. 1993), floating (Brown and Sherry 2008), and joining mixed species flocks (Ewert and Askins 1991, Latta and Wunderle 1996, Gram 1998, Jones et al. 2000, Warkentin and Morton 2000, Pomara et al. 2007) during the non-breeding season. These behavioral strategies may be influenced by gender, food availability (Brown and Sherry 2006), and/or intra- and inter-specific competition which may affect body condition and annual survival.

The Louisiana Waterthrush (*Parkesia motacilla*), hereafter waterthrush, is a large (19.6 ± 1.4 g) (Mattsson et al. 2009), monochromatic neotropical migratory warbler that breeds along first to third order perennial streams in deciduous and evergreen closed-canopy forests at medium to high gradients. They breed in the eastern United States from Wisconsin to central New England in the north to eastern Texas and northern Florida in the south. They overwinter throughout the Caribbean and Central America (Mattsson et al. 2009). Waterthrush have been used as indicators of stream integrity (O'Connell et al. 2003). Densities of breeding individuals are reduced along freshwater streams with macroinvertebrate communities compromised by stream acidification and anthropogenic land use changes (Mattsson and

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Cooper 2006, Muvihill et al. 2008, Mattsson et al. 2009). The breeding population of the waterthrush has remained stable and/or has slightly increased throughout its range (0.7%/yr, 1966–2007) (Sauer et al. 2008). Waterthrush occur along wooded freshwater streams throughout their non-breeding range (Eaton 1953). Master et al. (2002) suggested they are also riparian specialists during the non-breeding season inhabiting streams with characteristics similar to that of the breeding season.

We examined habitat use and behavioral strategies used by Louisiana Waterthrush during the non-breeding season. Our objectives were to quantify preferred habitat, describe on and off-stream habitat use, and ascertain if age affects habitat use. We made the following predictions: (1) waterthrush are riparian specialists occurring along headwater streams, and (2) they are territorial with older dominant individuals having smaller more resource-rich territories than younger individuals.

METHODS

Study Area.—This study was conducted along the Rio Sabana and a tributary at the northern boundary of the Caribbean National Forest in Sabana, Puerto Rico (18° 46' N, 66° 36' W). The Rio Sabana averages 9.3 m in width along this stretch with an average depth of 21 cm. The stream has riffles and rocks of varying sizes, an average flow rate of 0.20–0.26 m/sec, and a mostly closed canopy of mature trees; some stretches are through a residential part of Sabana. The amount of forest cover surrounding this portion of the watershed varies from contiguous forest to open areas with housing development.

Field Procedures.—Waterthrush were captured between 15 January and 15 February using playback recordings and mist nets placed in highly used flight paths. Birds exhibited low response to playback, and most captures occurred with mist nets placed across streams. All individuals were banded with a unique color band combination (2 color bands and a USGS aluminum band), and classified to age using plumage characteristics (Pyle 1997). No unbanded birds were observed after the capture period was completed. All individuals ($n = 22$) were fitted with radio transmitters (0.36 g; Model LB-2N, Holohil Systems Ltd., ON, Canada) attached with a cotton string harness to ensure they would degrade prior to spring migration (Hallworth et al.

2009). Home ranges were quantified by collecting a minimum of 50 (Seaman et al. 1999) locations with a Garmin 72 or 76 handheld global positioning system (GPS) (Olathe, KS, USA). Individuals were located via homing and followed for 2 consecutive hours taking locations at 5-min intervals daily for the life of the transmitter (~ 12 days). Five-min sampling intervals were chosen so birds were able to switch between foraging substrates and/or could traverse their home range during this time. Accuracy of home range delineation increases at shorter time intervals, despite the possible autocorrelation that may exist between bird locations (de Solla et al. 1999).

Ground and foraging substrates were quantified within 3-m radius plots at 12 randomly stratified bird locations based on the number of foraging observations within the different habitat types (stream and off stream), as well as six non-use locations created by randomly generated coordinates within individual home ranges. Plots were stratified by categorizing bird observations based on the habitat type used and randomly selected in proportion to use based on the number of total observations. We visually quantified the percent cover of mud, leaf litter, water, and vegetation within each plot. Percent canopy cover was quantified using a densitometer. We measured prey abundance at the center of each vegetation plot within a 1-m radius by recording all arthropods observed for 90 sec and then recording new individuals while turning over litter for an additional 90 sec. All arthropods were identified to Order. All stretches of streams were used, and we were not able to compare use and non use areas along streams. We classified percent cover of large rock (> 0.5-m diameter), medium rock (> 0.2–< 0.5-m diameter), gravel (rock < 0.2-m diameter), leaf litter (LL), vegetation (Veg), moss, roots and fallen coarse woody debris (Prop), and canopy cover (Canopy) were quantified along a 5-m stretch, if randomly stratified plot locations were within the stream. Width (m), flow rate (m/sec) and average depth (cm) of the stream were also quantified.

Statistical Analyses.—We used home range tools for ArcGIS (Rodgers et al. 2007) to calculate fixed-kernel use distributions (UD) from GPS locations for each individual. We used least squares cross validation (LSCV) to ascertain the smoothing parameter value (Barg et al. 2005). Use distributions of 95% were considered an individual's home range and UD's of 50% were

considered an individual's core area (Barg et al. 2005). The areal overlap of home range and core areas was quantified using Hawth's analysis tools for ArcGIS (Beyer 2004).

Akaike information criterion (AIC), corrected for small sample sizes (AIC_c ; Burnham and Anderson 2001), was used to evaluate models comparing habitat variables between use and non-use areas. We chose seven biologically relevant variables on the basis of field observations which included percent muddy substrate (Mud), percent leaf litter (LL), percent prop roots and fallen coarse woody debris (Fallen), percent canopy cover (Canopy), percent standing/running water (Water), prey availability (Prey), and percent vegetation cover (Veg). Kullback-Leibler information and Akaike's information criterion, corrected for small sample sizes (AIC_c) (Burnham and Anderson 2001) were used to evaluate the models. The lowest ΔAIC_c value indicates the most parsimonious model. Thus, the model with the lowest ΔAIC_c value indicates goodness-of-fit to the data while minimizing the number of parameters in the model. Binary logistic regressions were calculated with JMP 8.0 (SAS Institute Inc. 2010).

Home range sizes were normally distributed despite low samples sizes (ASY: Shapiro-Wilks' = 0.872, $df = 13$, $P = 0.069$; SY: Shapiro-Wilks' = 0.972, $df = 6$, $P = 0.907$). Core area size was log transformed to meet the assumptions of normality. Home range and core area size were compared between age classes and location (Rio Sabana or its tributary) with a two-way ANOVA. A Chi-square contingency table was used to ascertain if number of overlapping individuals was contingent upon age of the individual. Variable importance weights (ΣWi) were calculated by summing the candidate model weights that included the variable (Burnham and Anderson 2001). Least square regression was used to examine the relationship between prey availability and individual body condition. Body condition was obtained from the residuals of a linear regression of mass and the first principal component from a principal component analysis using morphometric data to account for body size (Jakob et al. 1996). A Kruskal-Wallis test was used to identify differences in body condition between years due to small sample sizes within each year. Kolmogorov-Smirnov tests were used to compare body condition and habitat use between age classes. Pearson correlations were

used to identify the relationship between habitat use and individual body condition. A Chi-square contingency table was used to examine differences in habitat use between after-second-year (ASY) and second-year (SY) individuals. Arcsine square root transformations were used to normalize data collected as percentages. Prey abundance was log transformed to meet the assumptions of normality. We used $\alpha = 0.05$ for all statistical tests and data are presented as means \pm SE.

RESULTS

Twenty-two waterthrush were tracked during the 3 years, eight in 2005, seven in 2006, and seven in 2007. Fourteen were ASYs, six were SYs, and age of two could not be reliably classified. Males and females have similar plumage and were not distinguishable.

The number of location points obtained per individual ranged from 30 to 206 with a mean of 91.2 ± 10.6 . Home range size varied widely from 0.38 to 8.80 ha. The average home range and core area sizes were 3.03 ± 0.54 ha and 0.71 ± 0.14 ha, respectively. ASY (2.15 ± 0.44 ha) individuals had smaller home ranges than SYs (4.65 ± 1.24 ha: $F_{1,18} = 8.00$, $P = 0.013$). Core areas ranged from 0.07 to 2.14 ha. Older individuals (ASYs) had smaller core areas than younger (SY) individuals ($F_{1,18} = 8.53$, $P = 0.011$). Neither home range ($F_{1,18} = 2.55$, $P = 0.131$) or core area ($F_{1,18}$, $P = 0.181$) size differed between the Rio Sabana and its tributary when accounting for the age of the individual. The extent of home range overlap varied between 0 and 71.5% with a mean overlap of $20.5 \pm 5.03\%$. The home ranges of ASYs ($24.6 \pm 6.67\%$) had more overlap than the home ranges of SYs ($4.10 \pm 2.20\%$; $t = 2.31$, $df = 17$, $P = 0.03$). The mean percent overlap of core areas was $6.45 \pm 2.66\%$ and did not differ between age classes ($t = 0.92$, $df = 17$, $P = 0.37$). Neither the number of overlapping home ranges ($X^2_3 = 3.75$, $P > 0.05$) nor core areas ($X^2_2 = 2.43$, $P > 0.05$) differed between ASYs and SYs. The density of waterthrush during the study ranged from three to five individuals/km and was estimated more accurately in our study through use of radio transmitters.

Waterthrush foraged mostly along streams ($64 \pm 7\%$) followed by muddy substrate ($27 \pm 6\%$). A small proportion of the time foraging was in housing developments ($7 \pm 5\%$) or on nearby roads ($2 \pm 1\%$). After-second year individuals spent more time foraging along streams and

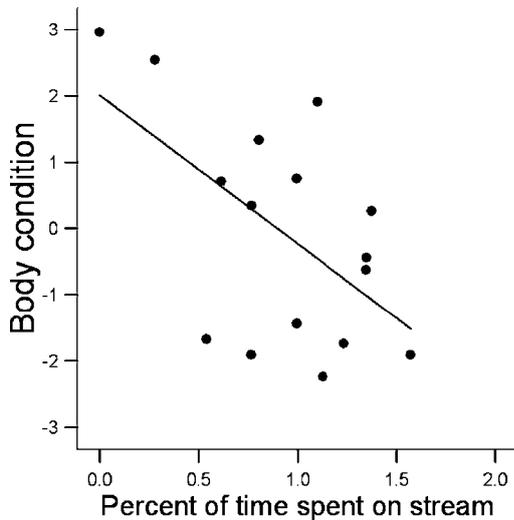


FIG. 1. The amount of time (transformed using arcsine square root to normalize the data) Louisiana Waterthrush foraged along streams in the Caribbean National Forest, Puerto Rico was negatively correlated with body condition ($r = 0.57$, $t = 2.56$, $df = 15$, $P = 0.02$).

muddy substrates than expected and avoided foraging along roads and in housing developments ($\chi^2_3 = 10.7$, $P = 0.01$). Second-year individuals spent more time foraging along roads and in housing developments than expected while foraging less along streams and muddy substrates than expected ($\chi^2_3 = 10.7$, $P = 0.01$).

Mean body condition of individuals did not differ between years (Kruskal Wallis = 0.95, $df = 2$, $P = 0.62$). Body condition did not differ between ASYs and SYs (Kolmogorov-Smirnov $Z = 0.936$, $P = 0.35$). Individual body condition was not dependent upon prey availability within their home range ($r^2 = 0.07$, $t = 0.68$, $df = 7$, $P = 0.53$). Prey availability was not correlated with home range ($r = 0.35$, $t = 1.21$, $df = 7$, $P = 0.26$) or core area size ($r = 0.27$, $t = 0.89$, $df = 7$, $P = 0.40$). Body condition was negatively correlated with amount of time foraging along the stream ($r = 0.57$, $t = 2.56$, $df = 15$, $P = 0.02$; Fig. 1). Body condition was not correlated with amount of time foraging in muddy substrates ($r = 0.13$, $t = 0.49$, $df = 15$, $P = 0.63$). Body condition was not influenced by the size of the home range ($r^2 = 0.12$, $t = 1.73$, $df = 14$, $P = 0.21$) or core area ($r^2 = 0.13$, $t = 1.50$, $P = 0.16$) overlap.

Prey availability ($\Delta AIC_c = 0.00$) was the most parsimonious model that distinguished use from non-use locations. Increased prey availability and

TABLE 1. Habitat variables that characterize use and random non-use locations of foraging Louisiana Waterthrush in the Caribbean National Forest, Puerto Rico. The lowest ΔAIC_c value indicates the model that best balances goodness-of-fit while minimizing the number of parameters in the model. W_i indicates the ranked model weights. Prey availability and percent leaf litter (LL) were selected as the two variables that best explain habitat use of Louisiana Waterthrush.

Model	AIC_c	ΔAIC_c	W_i
Prey	13.09	0.00	0.542
LL, Prey	14.91	1.82	0.218
Mud, Prey	16.40	3.31	0.103
LL, Water, Prey	17.00	3.91	0.077
Mud, LL, Prey	18.17	5.08	0.043
Mud, LL, Water, Prey	20.43	7.33	0.014
Mud, LL, Water, Prey, Veg	23.05	9.96	0.004
Mud, LL, Fallen, Canopy, Water, Prey, Veg	27.27	14.18	0.000
Mud, Canopy, Veg	37.57	24.48	0.000
Mud, LL, Water, Veg	44.84	31.74	0.000

a lower percent of leaf litter cover ($\Delta AIC_c = 1.82$) also were parsimonious with respect to use and non-use locations (Tables 1, 2). Two additional models that provided moderate support ($2 \geq \Delta AIC_c \leq 4$) included higher percent of muddy substrate and increased prey availability ($\Delta AIC_c = 3.31$), and lower percent of leaf litter cover, higher percent of standing water, and increased prey availability ($\Delta AIC_c = 3.91$). Prey availability ($\Sigma W_i = 1.00$) was the single most important variable that distinguished use from non-use locations. Prey availability was higher along streams and in muddy substrates than non-use locations ($F_2 = 7.9$, $P = 0.002$; Fig. 2). Prey availability did not differ between stream and muddy substrates (t -stat = 0.13, $df = 16$, $P = 0.90$). The entire length of the Rio Sabana and its tributary was used by waterthrush during the study, and we were unable to compare use and non-use stream variables.

DISCUSSION

Waterthrush secured fixed home ranges that encompassed multiple habitat types. Home ranges exhibited a wide range of overlap with neighboring individuals although there was minimal overlap of core areas. This overlap did not affect body condition. There was greater overlap among ASYs despite having smaller home ranges. This may be the result of older birds occupying higher quality habitats both along and away from

TABLE 2. Values ($\bar{X} \pm \text{SE}$) measured in 3-m radius plots for mud, leaf litter, water, and vegetation at Louisiana Waterthrush foraging and random non-use locations presented as percent ground cover in the Caribbean National Forest, Puerto Rico.

	Mud	Leaf litter	Water	Vegetation	Canopy	Prey
Use	38.8 \pm 4.89	43.5 \pm 4.12	11.7 \pm 2.69	47.9 \pm 3.60	87.0 \pm 3.11	8.04 \pm 0.73
Non-use	1.04 \pm 0.58	91.7 \pm 1.99	3.13 \pm 2.92	48.1 \pm 5.07	94.7 \pm 0.35	5.26 \pm 1.24

streams. ASYs did not apportion greater percentages of time along streams than SYs but older birds did use streams more than expected based upon availability whereas younger birds spent more time along roads and within housing developments than expected. These results suggest older birds assert dominance over younger individuals and secure the highest quality habitat. Conspecific aggression was observed when two individuals crossed paths, and these encounters were only observed along streams (MTH, pers. obs.). Waterthrush, like Ovenbirds (*Seiurus aurocapilla*), may maintain and defend smaller territories through active defense of core areas and during chance encounters with conspecifics (Brown and Sherry 2008). ASYs had significantly smaller home ranges than SYs also suggesting older individuals are able to secure higher quality

home ranges (Holmes et al. 1996); however, neither home range nor core area size was correlated with prey availability. Roost sites (Smith et al. 2008) and cover (Watts 1991) may also influence home range size.

Waterthrush mostly foraged along streams but also used off-stream habitats with appropriate ground substrate, especially in areas with concentrated arthropod abundance. The most important ground feature in off-stream areas used for foraging was the amount of muddy substrate. Foraging locations had nearly 40% muddy ground cover compared to 1% in non-use areas. Northern Waterthrush (*Parkesia noveboracensis*) and Louisiana Waterthrush seek saturated soils that are often rich in arthropods (Smith et al. 2010). Foraging locations had less than half the leaf litter compared to non-use areas. There was nearly four times greater standing water and greater prey abundances in areas used for foraging. Waterthrush are ground foragers and attracted to moist substrates. Thus, when not along streams they seek areas where ground arthropods are in higher concentrations. Prey availability was the most parsimonious model that influenced habitat use, followed by a model containing prey availability and percent leaf litter. The importance of leaf litter is likely due to waterthrush actively searching for arthropods by flipping leaves as they forage both on and off stream (MTH, LRR, pers. obs.).

Individual body condition was negatively correlated with amount of time foraging along the stream which may be influenced by the amount of conspecific encounters and time spent defending core areas. Conspecific encounters and aggression were only observed along streams (MTH, LRR, pers. obs.). The riparian habitat in this study area has been affected by development which may have impacted water quality and stream invertebrate richness and abundance. The streams still attract waterthrush, but they may not have suitable conditions for invertebrate productivity.

Return rates (13–29%) in our study were low for a neotropical migrant when compared to

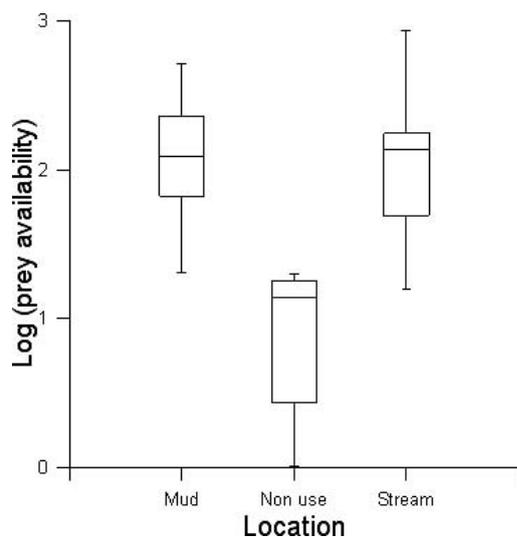


FIG. 2. Prey availability (log transformed to meet the assumptions of normality) was significantly greater in locations used (mud and stream) by Louisiana Waterthrush than randomly selected non-use locations within their home range (Non use). The box depicts the median (solid line in the box), lower and upper 25% quartiles, and whiskers represent the data range.

TABLE 3. Arthropods quantified during timed prey availability counts within a 1-m radius. Arthropods were quantified for a 90-sec observation period and then for an additional 90 sec while flipping over leaves to simulate the most common Louisiana Waterthrush foraging strategy. Data ($\bar{X} \pm SE$) are shown for the two most highly used substrates (stream and mud) as well as use and non-use locations.

Order	Stream	Mud	Use	Non-use
Diptera	3.48 ± 0.46	3.97 ± 1.19	2.93 ± 0.41	2.83 ± 0.62
Hymenoptera	0.82 ± 0.17	1.45 ± 0.39	1.24 ± 0.18	1.85 ± 0.6
Aranea	0.59 ± 0.1	0.87 ± 0.34	0.52 ± 0.1	0.44 ± 0.21
Platydesmida	0 ± 0	0.19 ± 0.17	0.1 ± 0.05	0.08 ± 0.05
Orthoptera	1.06 ± 0.28	0.22 ± 0.1	0.6 ± 0.17	0.9 ± 0.49
Lepidoptera	0.06 ± 0.02	0.13 ± 0.05	0.07 ± 0.02	0.08 ± 0.04
Odonata	0.01 ± 0.01	0 ± 0	0.01 ± 0.01	0 ± 0
Hemiptera	2.59 ± 0.82	0 ± 0	1.33 ± 0.48	0.03 ± 0.03
Pulmonata	0.07 ± 0.02	0.09 ± 0.05	0.06 ± 0.02	0.01 ± 0.01
Unidentified Larva	0.22 ± 0.06	0.24 ± 0.12	0.23 ± 0.06	0.03 ± 0.02

Prairie Warbler (*Dendroica discolor*) (50%) (Latta and Faaborg 2001), American Redstart (*Setophaga ruticilla*) (40–70%) (Marra and Holmes 2001), and Northern Waterthrush (14–52%) (Reitsma et al. 2002) during the non-breeding season. It was not possible to discern mortality from emigration. Use of radio transmitters may be a cause for the low return rates (see Mattson et al. 2006), but 59% of the birds with transmitters were recaptured and harnesses removed prior to spring departure. Use of cotton string as a harness increases the probability that transmitters are lost within 4–6 weeks of application, prior to migration (Hallworth et al. 2009).

Previous work on Louisiana Waterthrush during the non-breeding season suggests this species is a riparian specialist with similar habitat requirements to those used during the breeding season (Master et al. 2002). Our study suggests Louisiana Waterthrushes are not strictly associated with headwater streams and use a variety of habitat types including muddy substrates and housing developments. Food availability influenced habitat use of individuals although it did not appear to impact home range size or core area. Water quality parameters were not measured although Master et al. (2002) found the highest waterthrush densities (10 individuals/km) in Costa Rica occurred along streams with moderate to high abundance of macroinvertebrates.

Waterthrush use areas as far as 150 m from streams despite being closely associated with riparian habitats. Our study illustrates the importance of food availability for Louisiana Waterthrush and indicates this species uses a wider array of habitat types than previously thought. The

frequent use of saturated soils adjacent to rivers and streams as foraging sites is an important component to understanding their non-breeding distribution and, potentially, for considering this species' conservation throughout their wintering distribution.

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