



Roosting behavior of a Neotropical migrant songbird, the northern waterthrush *Seiurus noveboracensis*, during the non-breeding season

Joseph A. M. Smith, Leonard R. Reitsma, Larry L. Rockwood and Peter P. Marra

J. A. M. Smith (correspondence) and P. P. Marra, Smithsonian Migratory Bird Center, National Zoological Park, PO Box 37012 MRC 5503, Washington, DC 20013-7012, USA. E-mail: smithjam@gmail.com. – L. R. Reitsma, Plymouth State University, Dept. of Biological Sciences, Plymouth, NH 03264, USA. – L. L. Rockwood, George Mason University, Dept. of Environmental Science and Policy, Fairfax, VA 22030, USA.

Several species of Nearctic–Neotropical migratory songbirds appear to form roosting aggregations while on their wintering grounds but little is understood about the ecology of this behavior. We studied roosting behavior and patterns of roost habitat selection in the northern waterthrush *Seiurus noveboracensis*, during three winter years (2002–2004) in Puerto Rico using radio telemetry. Overall, red mangrove was selected for roosting disproportionately to its availability. Regardless of diurnal habitat used, 87% ($n = 86$) of northern waterthrush selected dense stands of coastal red mangrove for roost sites. Individuals traveled up to 2 km to access roost sites in this habitat on a daily basis. The majority (8 of 14) of individuals roosted alone, while others roosted in loose aggregations near communal roosts of gray kingbirds *Tyrannus dominicensis*. Patterns of roost site selection did not vary by sex. Individuals showing aggressive response to playback during the day, however, selected roost sites significantly closer to the coast. Several additional migratory and resident bird species also used red mangrove for night-time roosting habitat. Red mangrove may be a critical nocturnal roosting habitat for bird populations that live in proximity to coastal areas in the Neotropics. The benefits of nocturnal roosting behavior as well as why individuals appear to select red mangrove remain poorly understood.

Roosting behavior is poorly understood in many bird species. The majority of detailed studies have focused on species that form conspicuous communal roosts. Communal roosting has been documented in numerous species of passerine birds in temperate areas (especially Icteridae, Sturnidae, and Corvidae; Allen and Young 1982, Eiserer 1984), but roosting behavior in wintering long-distance migratory passerines has only been documented in a few cases and has rarely been studied.

Evidence is building that Nearctic–Neotropical migratory songbirds move to nocturnal roosting sites disjunct from individual territories or home ranges while on their non-breeding grounds. A summary of these reports across a broad geographic area within the non-breeding range reveals a common pattern of off-home range movements to roost sites by a diversity of species. Most evidence consists of anecdotal observations of unmarked individuals moving away from diurnal activity areas at dusk. This type of roosting behavior has been observed in gray catbird *Dumetella carolinensis* (Alsop 1995), northern parula *Parula americana*, Cape May warbler *Dendroica tigrina*, prairie warbler *Dendroica discolor* (Stacier 1992, Baltz 2000, Latta 2003), palm warbler *Dendroica palmarum* (Latta 2003), prothonotary warbler *Protonotaria citrea* (Morton 1980, Warkentin and Morton 1995), and northern waterthrush (Reitsma et al. 2002, Burson et al. 2005, Hunt et al. 2005).

Little is understood about the factors that drive this behavior and what function it might serve. Needed are in-depth within species studies that describe the basic ecology of roosting behavior and quantify its prevalence in individually marked birds.

In this study we describe the winter roosting behavior of the northern waterthrush in eastern Puerto Rico using radio telemetry. Specifically, we determined patterns of habitat and site selection, roost site fidelity, the prevalence of communal roosting, and the role of demographic and behavioral variables in explaining variation in roosting behavior.

Methods

Study species

The northern waterthrush is a ground-feeding paruline warbler that breeds in North America throughout Canada, the Northeastern United States and Alaska and winters in the Neotropics in Central America, northern South America and the Caribbean (Eaton 1995). During the non-breeding period the waterthrush is site-faithful and solitary during the day (Schwartz 1964, Lefebvre et al. 1994) and is considered to be a mangrove and wet habitat

specialist (Wunderle and Waide 1993). Non-breeding territoriality 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 (unpublished data).

Study area

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 3,464 ha that compose the station, 1612 are second growth dry forest, 769 are mangrove forest, and 1083 are developed (GIS data, Eagan, McAllister and Associates, Inc. 1998). Developed areas are composed of roads, an airstrip, residential areas, office complexes, commercial properties, and a ship port.

Our research was conducted in four habitat types including second-growth dry forest and three mangrove forest types dominated by single species: black mangrove *Avicennia germinan*, 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). 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 for diurnal bird capture consisted of two white mangrove sites 6.5 km apart, two black mangrove sites 1.5 km apart, two dry forest sites 1.5 km apart, and one red mangrove site. Canopy heights within each site ranged from 3–20 m. All mangrove sites had standing water, usually less than 1 m in January, but water depth gradually decreased as the dry season progressed in spring towards April and May. Daily fluctuations in moisture levels infrequently occurred in coastal red mangrove areas during periods of exceptional tide fluctuations. Dry forest sites did not have standing water.

Data collection

Northern waterthrush were captured in late January, mid-February, and early March. We erected ten to fifteen 12 m mist nets in each habitat type for a two-day period from 08.00 to 16.00 AST. 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) and weighed to the nearest ± 0.1 g using an Ohaus digital scale. A 50 μ l blood

sample was taken to determine sex using polymerase chain reaction (Griffiths et al. 1998). Age was not determined due to the unreliability of ageing methodology for this species during the winter period (Pyle 1997). Only individuals captured at least one hour after sunrise were used in this study to maximize the probability that they were using the habitat in which they were captured and not in commute from a roost location. Each individual was fitted with a radio transmitter with a unique frequency ($n = 86$; Holohil BD2-A, 0.74 g) using the leg harness technique (Rappole and Tipton 1991). Transmitter life ranged from three to four weeks. We used radio receivers (Advance Telemetry Systems, Fieldmaster 16), and 3 element Yagi antennas to relocate individuals with transmitters.

Roost sites were located at night at least five days after initial capture by homing no closer than 5 m to birds with transmitters to ensure that they were not disturbed. The position of the bird was confirmed by short-range triangulation. We marked the observer location with a Global Positioning System (Garmin GPS 12) and noted the distance and bearing to the roost tree. To quantify diurnal habitat use, diurnal locations were acquired using the same methodology, with one location per day acquired for the 3–4 week estimated life of the transmitter. Minimum convex polygons were created around these locations to determine the center (centroid) of diurnal home ranges so that distance to roost could be calculated.

To determine whether roost sites were communal, a subset ($n = 14$) of individuals were observed at roost sites using a thermal imaging device (Raytheon X-100) in 2004. Thermal imaging devices convert the far-infrared radiation that is produced by heat into a visible image composed of gradients and contrasts in temperature. Since birds are significantly warmer than their surroundings, they are easily detectable at night with such a device. Once located in the tree with the thermal imager, each bird was spotlighted with a flashlight to confirm identity by reading color bands. The area surrounding the roost site of birds with transmitters was scanned with the thermal imager both upon approach and upon arrival to the roost site to determine the presence and quantity of other roosting birds. These other birds were spotlighted to confirm species identity. Individuals were considered to be roosting alone if no other birds were observed within 5 m of the roost site used by the target individual.

To quantify roost site fidelity within a season, we relocated a different subset ($n = 25$) of individuals at roost sites a second time approximately two weeks after the initial location. Birds flushed from roost sites on initial visits and those observed with the thermal imager were not included in this set to eliminate the possibility that roosts changed due to disturbance.

We returned to roost sites during the day to record habitat measurements. In a 5 m diameter circular plot surrounding the site we measured canopy cover using a spherical densiometer (Forestry Suppliers Model A), average canopy height using a clinometer, and ground cover using the point-intercept technique (Bonham 1989). Additionally we measured the diameter of each tree within the plot, noted species composition, and measured water depth at the center of the plot. These same measurements were taken

within diurnal home ranges at a randomly selected diurnal telemetry location point for each individual.

To estimate con-specific aggression of birds with transmitters on diurnal home ranges, we presented each individual with a 10-min chip vocalization playback (Marra 2000). Based on the results of previous studies with non-breeding territorial migrants, such presentations can reveal gradients in aggression corresponding to competitive ability that often vary by sex and age class (Rappole and Warner 1980, Stutchbury 1994, Neudorf and Tarof 1998, Marra 2000). To make playback presentations we located birds by homing with radio telemetry to approximately 15 m. Presentations were made between 09.00 and 15.00 h to ensure that the bird was on its diurnal activity area rather than moving to or from roost. The response was classified as either positive (target bird vocalized and approached decoy to within 10 m or less) or negative (remained silent and held position or moved away from playback).

Overall habitat availability on Naval Station Roosevelt Roads was calculated using Ikonos 1m resolution satellite imagery of the naval station. Data were ground-truthed using data derived from a concurrent study of the diurnal habitat use of northern waterthrush. Black mangrove and white mangrove were classified as a single type because they could not be reliably distinguished using satellite imagery.

Results

In total, 87% of northern waterthrush ($n = 75/86$) moved from diurnal home ranges to discrete roosting locations while the remainder roosted on diurnal home ranges (Fig. 1). The exact timing of movements was not quantified for individuals, but departures generally occurred within one h of sunset based on mist netting data collected from late afternoon through 30 min after sunset. Similarly, birds returned to diurnal home ranges in the morning, generally within one h after sunrise.

Distances traveled to roost sites ranged from a minimum of several m for those individuals that did not leave diurnal home ranges to a maximum distance of two km. Routes to roost sites often required birds to move across roads, areas of development, and extensive habitat types not typically used by this species including mud flats and sparse short (<2 m) black mangrove. Routes to and from roost sites, however, tended to be along corridors of taller vegetation which produced a funneling of many individuals through particular areas. Movements to roost appeared to be direct. Radio transmitter signals would fade quickly as birds departed, suggesting that movements were rapid. Behavior returning from roost sites was less clear as we were unable to monitor birds during departure from roost sites. The only mortality observed during this study was an individual which was killed by a car while crossing a road in the morning during transit from roost site to its diurnal home range.

Site fidelity

All individuals exhibited strong site fidelity to roost trees (100%, $n = 25$) over the two week re-location period

regardless of whether they remained on diurnal home ranges or moved to a discrete location. Five individuals were recaptured and then tracked in two successive years. Four of these were faithful to roost sites between years, while one roosted 65 m from the previous years' site. Interestingly, two other individuals that were accidentally flushed from their roost sites did change roost locations within a season. One individual moved 100 m from the initial location when relocated two weeks later and the other moved 1.7 km from the initial roost site location.

Habitat selection

Pure stands of red mangrove were used for roosting by 87% ($n = 86$) of individuals regardless of the diurnal habitat used. While northern waterthrush primarily spend daylight hours on the ground (Eaton 1995), roost sites were always located in trees. All individuals using dry forest ($n = 35$) and red mangrove habitats ($n = 11$) during the day selected red mangrove for roost sites. The majority of individuals using white mangrove (90%, $n = 19$) and over half of the individuals using black mangrove (57%, $n = 21$) also selected red mangrove to roost. Those that did not select red mangrove to roost remained on diurnal activity areas.

Compared to diurnal habitats, roost sites in red mangrove had significantly greater canopy cover ($z = -6.8$, $P < 0.001$; Wilcoxon signed rank test with Bonferroni correction), and standing water ($z = -5.9$, $P < 0.001$). Basal area ($z = -0.8$, $P = 0.42$), and canopy height ($z = -2.1$, $P = 0.04$) did not differ significantly between roost site and home range locations. Individuals did not use roost trees that were less than 2.5 m in height ($n = 53$). For individuals roosting in black and white mangrove, none of these habitat traits differed significantly from diurnal locations in these same habitats (Wilcoxon signed rank test, $P > 0.05$).

Red mangrove habitat composes 4.8% (116 ha) of the total forested area at Roosevelt Roads Naval Station and 15% of the total mangrove area. This habitat was selected for roosting disproportionately to its availability ($X^2 = 1261$, $df = 2$, $P < 0.001$; Fig. 1).

Traits associated with roosting

Individuals responding aggressively to playback also tended to occupy roost sites in red mangrove that were significantly closer to the coast (Aggressive = 7.7 ± 10.3 m, $n = 10$, non-aggressive = 49.9 ± 7.2 m, $n = 23$, ANOVA $F = 9.4$, $df = 1$, $P < 0.005$; Fig. 3) although distance to coast from the center of diurnal home ranges did not differ significantly (Aggressive = 469.2 ± 124.6 m, non-aggressive = 540.2 ± 74.5 m, $F = 0.27$, $df = 1$, $P = 0.607$). Males and females exhibited no significant spatial segregation with respect to distance of roost sites from the coast, but males did tend to be closer ($\text{♂} = 18.8 \pm 8.2$ m, $n = 16$, $\text{♀} = 52.0 \pm 9.4$ m, $n = 17$, ANOVA $F = 3.1$, $df = 3$, $P < 0.089$). There was no significant interaction effect between sex and level of aggression (ANOVA $F = 1.0$, $df = 3$, $P < 0.324$).

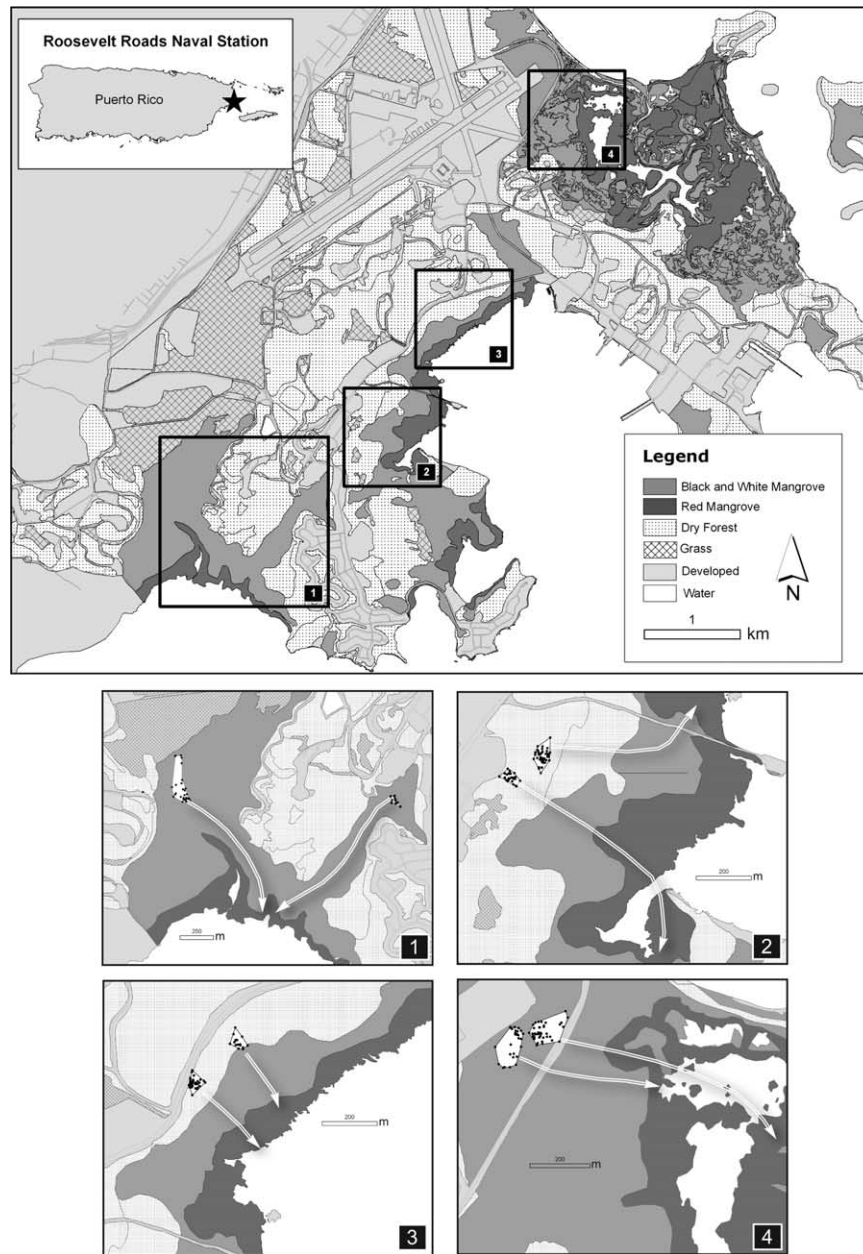


Figure 1. Examples of movements for 8 individuals between diurnal activity areas and red mangrove roost sites for black mangrove (inset 1), dry forest (insets 2 and 3), and white mangrove (inset 4). Points are individual telemetry locations which are bounded by minimum convex polygons representing diurnal home ranges. Arrows indicate inferred paths to roost sites.

Roosting aggregation

During the three years of this study, 12 different radio tracked individuals (5 observed with thermal imager) roosted at the periphery of communal gray kingbird *Tyrannus dominicensis* roosts. All gray kingbird roosts were located in red mangrove stands and were typically less than 10 m from the coast. gray kingbird roosts appeared to be temporally and spatially stable during the 3 study years and all were composed of 20, or greater kingbirds in either a single tree or a contiguous clump of trees.

All observed roosting aggregations of northern waterthrush were in red mangrove. Of individual waterthrushes observed with a thermal imager, 6 of 14 roosted within 3 m of 1 to 12 conspecifics. All but one of these aggregations

were at the periphery of communal roosts of gray kingbird *Tyrannus dominicensis*. The remainder ($n = 8$) roosted solitarily, with no other birds evident upon scanning nearby vegetation within 10–15 m of the focal roost tree with the thermal imager.

Northern waterthrush and other paruline warblers incidentally observed at roost sites with the thermal imager appeared unaware of our presence, even after they were spotlighted to confirm identity. In contrast, gray kingbirds were alert and vocal upon the approach of observers within 25 m of the roost.

Anecdotal evidence and observations of other migratory and resident species at roost sites were also made. During dawn and dusk mist netting sessions at habitat corridors we had high capture rates of other species including prairie

warbler *Dendroica discolor*, northern parula *Parula americana*, prothonotary warbler *Protonotaria citrea*, gray kingbird *Tyrannus dominicensis*, and greater Antillean grackle *Quiscalus niger*. Nets were oriented parallel to the coast and captures were always unidirectional, with birds heading toward the coast in the evening (primarily after sunset) and heading away from the coast in the morning (primarily before sunrise). Additionally, individuals of each species were incidentally observed with the thermal imager at red mangrove roost sites. With the exception of grackles and kingbirds, no aggregations of the migrant species were ever found during our efforts to find waterthrush roosts.

Discussion

Northern waterthrushes exhibited strong selection for roost sites in red mangrove habitats and were faithful to these roost sites within seasons and between years. Individual birds often flew considerable distances and through seemingly poor habitat types to move between roost sites in red mangrove at dusk and diurnal home ranges at dawn.

In contrast to gray kingbirds and greater Antillean grackles which aggregate in large numbers in single trees while roosting in Puerto Rico (Post 1982), most waterthrushes roosted alone, although a few were aggregated and typically spaced 1 to 3 m apart. In the latter case when waterthrushes were observed roosting in close proximity to conspecifics this tended to be at the periphery of kingbird roosts. The tendency of northern waterthrush to associate with a species which appears to be more alert at night may deserve further consideration. Similar mixed-species breeding aggregations have been shown to confer predator protection benefits to one nesting species by its reliance on another nesting species' heightened levels of vigilance or defensive behavior (Burger 1984, Richardson and Bolen 1999, Quinn 2003). Such patterns could also exist among roosting birds.

Three hypotheses have been proposed to explain why roost aggregations occur in birds: 1) information sharing, 2) thermoregulatory benefits, and 3) predator avoidance (Eiserer 1984, Beauchamp 1999). The information sharing hypothesis proposes that roost members share information about the location of resources and primarily applies to diurnally social species during the non-breeding season that seek out patchy resources (Fischl and Caccamise 1987, Wright et al. 2003). The second hypothesis involving thermoregulation may not seem likely for birds wintering in lowland tropical areas but selection of sheltered microsites may confer some benefit (Merola-Zwartjes 1998). Northern waterthrush lose an average of 6% of their body mass at night (Smith et al. unpubl. data). It is possible that red mangrove, with its proximity to water and dense canopy may minimize this mass loss by blocking wind and rain and maintaining warmer nocturnal temperatures. Finally, although we have no direct evidence to support, or refute hypothesis 3)-predator avoidance-red mangroves inundated by water may present a barrier to predators from adjacent terrestrial habitats. Overall, however, fewer nocturnal predators exist in the Caribbean compared to mainland tropical areas (Vitousek 1988). In sum, we still do not have a clear understanding as to why this species exhibits roosting

behavior during the non-breeding season. Additional research testing some of the above hypotheses is needed.

The fact that individuals exhibited strong habitat selection for red mangrove over other more available habitats, and that this selection was mirrored by a range of species suggests that roost habitats could differ in suitability and could also be limiting. We have no data at this time to support or refute this idea. Support for this hypothesis, however, was our finding that roosts closer to the coast were more often occupied by aggressive northern waterthrush individuals suggesting that there may be competition for roost sites within species. Several previous studies of passerine species have demonstrated that dominant individuals use aggressive behavior to acquire and maintain higher quality roost sites (Rohwer 1977, Weatherhead and Hoysak 1984, Summers et al. 1987, Feare et al. 1995, Calf et al. 2002, Mezquida et al. 2005). As we begin to understand what once appeared to be a novel behavior, our priority should be to determine if and how these roost sites differ in suitability and the extent to which this habitat might be limiting (Fretwell 1980).

The phenomenon of roosting in red mangrove appears to be broad, with evidence for the behavior across the Caribbean (Stacier 1992, Latta 2003), and into Central America (Warkentin and Morton 1995). In light of these findings, the conservation value of coastal red mangrove areas cannot be understated. Conservation planners should consider measures to ensure that connectivity is maintained between inland and coastal mangrove habitats to provide suitable passage routes between diurnal and nocturnal sites and that remaining areas of red mangrove throughout Central America and the Caribbean become a high priority for protection given their importance for a suite of migratory and resident bird species.

Acknowledgements – This research was supported by a grant from DoD Legacy Resources Management Program. We thank Daniel Brown, Ram Papish, Ryan Peters, Mark Pollock, TJ Robinson, and Jared Woodcock for their excellent and dedicated work in the field. Additional long hours and able field assistance were provided by Alicia Byrd, Sara Campbell, Bill Deluca, Brian Gibbons, and Karin Roux. We thank Winston Martinez and Oscar Diaz for facilitating our work at Roosevelt Roads Naval Station and the U.S. Forest Service Sabana Field Station and its staff for providing lodging and laboratory space. Todd Crowl generously loaned us a kayak which became an essential tool in our roost finding efforts. Lee Weight at the Smithsonian Museum Support Center provided lab space and indispensable guidance during analysis of blood samples. Finally we thank Jean Lodge and Joe Wunderle for all of the assistance and hospitality they extended during our stay in Puerto Rico.

References

- Allen, H. L. and Young, L. S. 1982. An annotated bibliography of avian communal roosting. – Washington State Game Department, Olympia, Washington.
- Alsop, F. J. III. 1995. A communal roost of gray catbirds at Eco Pond, Everglades National Park. – Florida Field Nat. 23: 69.
- Baltz, M. E. 2000. The non-breeding season ecology of neotropical migratory birds in the dry zone of Puerto Rico. – PhD dissertation, University of Missouri, Columbia.

- Bonham, C. D. 1989. Measurements for terrestrial vegetation. – Wiley-Interscience, New York.
- Burger, J. 1984. Grebes nesting in gull colonies-protective associations and early warning. – *Am. Nat.* 123: 327–337.
- Burson, S. L., Reitsma, L. R. and Hunt, P. D. 2005. Conservation implications of multiple habitat use by northern waterthrush during the nonbreeding season. – *J. Caribb. Ornithol.* 18: 72–76.
- Calf, K. M., Underhill, L. G., and Slowtow, R. 2002. Dominance and huddling behavior in bronze mannikin (*Lonchura cucullata*) flocks. – *Ibis* 144: 495–508.
- Eaton, S. W. 1995. Northern waterthrush (*Seiurus noveboracensis*). – In: Poole, A. and Gill, F. (eds). The birds of North America, No. 182. Academy of Natural Sciences. Philadelphia, and American Ornithologists' Union, Washington, DC..
- Eiserer, L. A. 1984. Communal roosting in birds. – *Bird Behav.* 5: 61–80.
- Ewel J. J. and Whitmore, J. L. 1973. The ecological life zones of Puerto Rico and the U.S. Virgin Islands. – U.S. Forest Service Research Paper ITF-18. Institute of Tropical Forestry. Rio Piedras, Puerto Rico.
- Feare, C. J., Gill, E. L., McKay, H. V. and Bishop, J. D. 1995. Is the distribution of starlings *Sturnus vulgaris* within roosts determined by competition? – *Ibis* 137: 379–382.
- Fischl, J. and Caccamise, D. F. 1987. Relationships of diet and roosting behavior in the european starling. – *Am. Midl. Nat.* 117: 395–404.
- Fretwell, S. 1980. Evolution of migration in relation to factors regulating bird numbers. – In: Keast, A. and Morton, E. S. (eds). Migratory birds in the neotropics: ecology, behavior, and conservation. Smithsonian Institution Press, Washington D.C., pp. 517–527.
- Griffiths, R., Double, M., Orr, K. and Dawson, R. 1998. A simple DNA test to sex most birds. – *Mol. Ecol.* 7: 1071–1076.
- Hunt, P. D., Reitsma, L. R., Burson, S. L. and Steele, B. B. 2005. Spatial and temporal distribution of northern waterthrushes among nonbreeding habitats in southwestern Puerto Rico. – *Biotropica* 37: 697–701.
- Latta, S. C. 2003. Effect of scaly-leg mite infestations on body condition and site fidelity of migratory warblers in the Dominican Republic. – *Auk* 120: 730–743.
- Lefebvre, G., Poulin, B., and McNeil, R. 1994. Spatial and Social Behavior of Nearctic Warblers Wintering in Venezuelan Mangroves. – *Can. J. Zool.* 72: 757–764.
- Marra, P. P. 2000. The role of behavioral dominance in structuring patterns of habitat occupancy in a migrant bird during the nonbreeding season. – *Behav. Ecol.* 11: 299–308.
- Merola-Zwartjes, M. 1998. Metabolic rate, temperature regulation, and the energetic implications of roost nests in the bananaquit (*Coereba flaveola*). – *Auk* 115: 780–786.
- Mezquida, E. T., Villaran, A. and Pascual-Parra, J. 2005. Microhabitat use and social structure in linnet *Carduelis cannabina* and corn bunting *Miliaria calandra* at a winter roost in central Spain. – *Bird Study* 52: 323–329.
- Morton, E. S. 1980. Adaptations to seasonal changes by migrant landbirds in the Panama Canal Zone. – In: Keast, A. and Morton, E. S. (eds). Migratory birds in the Neotropics: ecology, behavior, and conservation. Smithsonian Institution Press, Washington D.C., pp. 437–453.
- Neudorf, D. L. and Tarof, S. A. 1998. The role of chip calls in winter territoriality of yellow warblers. – *J. Field Ornithol.* 69: 30–36.
- Post, W. 1982. Why do grey kingbirds roost communally? – *Bird Behav.* 4: 46–49.
- Pyle, P. 1997. Identification Guide to North American Birds. – Slate Creek Press, Bolinas.
- Quinn, J. L., Prop, J., Kokorev, Y. and Black, J. M. 2003. Predator protection or similar habitat selection in red-breasted goose nesting associations: extremes along a continuum. – *Anim. Behav.* 65: 297–307.
- Rappole, J. H. and Tipton, A. 1991. New harness design for attachment of radio transmitters to small passerines. – *J. Field Ornithol.* 62: 335–337.
- Rappole, J. H. and Warner, D. W. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. – In: Keast, A. and Morton, E. S. (eds). Migratory birds in the neotropics: ecology, behavior, distribution, and conservation. Smithsonian Institution Press, Washington, DC., pp. 353–393.
- Reitsma, L., Hunt, P., Burson, S. L. and Steele, B. B. 2002. Site fidelity and ephemeral habitat occupancy: northern waterthrush use of Puerto Rican black mangroves during the nonbreeding season. – *Wilson Bull.* 114: 99–105.
- Richardson, D. S. and Bolen, G. M. 1999. A nesting association between semi-colonial Bullock's orioles and yellow-billed magpies: evidence for the predator protection hypothesis. – *Behav. Ecol. and Sociobiol.* 46: 373–380.
- Rohwer, S. A. 1977. Status signaling in harris sparrow: some experiments in deception. – *Behavior* 61: 107–129.
- Schwartz, P. 1964. The northern waterthrush in Venezuela. – *Living Bird* 3: 169–184.
- Stacier, C. A. 1992. Social behavior of the northern parula, Cape May warbler, and prairie warbler wintering in second-growth forest in southwestern Puerto Rico. – In: Hagan, J. M. and Johnston, D. W. (eds). Ecology and conservation of neotropical migrant landbirds. Smithsonian Institution Press, Washington D.C., pp. 309–320.
- Stutchbury, B. J. 1994. Competition for winter territories in a neotropical migrant-the role of age, sex and color. – *Auk* 111: 63–69.
- Summers, R. W., Westlake, G. E. and Feare, C. J. 1987. Differences in the ages, sexes and physical condition of starlings *Sturnus vulgaris* at the center and periphery of roosts. – *Ibis* 129: 96–102.
- Vitousek, P. M. 1988. Diversity and biological invasions of oceanic islands. – In: Wilson, E. O. and Peters, F. M. (eds). Biodiversity. Natl. Acad. Press, Washinton D.C., pp. 181–189.
- Warkentin, I. G. and Morton, E. S. 1995. Roosting behavior of prothonotary warblers in the non-breeding season. – *Wilson Bull.* 107: 374–376.
- Weatherhead, P. J. and Hoysak, D. J. 1984. Dominance structuring of a red-winged blackbird roost. – *Auk* 101: 551–555.
- Wright, J., Stone, R. E. and Brown, N. 2003. Communal roosts as structured information centres in the raven, *Corvus corax*. – *J. Anim. Ecol.* 72: 1003–1014.
- Wunderle, J. M. Jr. and Waide, R. B. 1993. Distribution of overwintering nearctic migrants in the Bahamas and Greater Antilles. – *Condor* 95: 904–933.