Population Ecology and Foraging Behavior of Breeding Birds in Bottomland Hardwood Forests of the Lower Roanoke River

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(Abstract)

Nest survival often is lower at habitat edges than in habitat cores because of greater nest predation and parasitism near edges. I studied nest survival of breeding birds in bottomland hardwood forests of the lower Roanoke River, North Carolina. Nesting success was monitored in two forest width classes: narrow bands of levee forest that were dominated by two edge types, and wide, continuous levee forest stands that have edges but most forest is relatively far from edge. Nest success of Acadian Flycatchers and Prothonotary Warblers was similar in narrow and wide levees; nest success of Northern Cardinals was greater in narrow levees. Results of my study indicate that edge effects are not universal, and that amount of contrast at edges may interact with landscape context to alter ecological processes, such as nest predation.

Bird populations are remarkably constant over time relative to other taxa, implying strong regulation. Avian population ecologists, however, have not studied regulatory mechanisms as often as seasonal limiting factors. Conversely, avian behavioral ecologists seldom emphasize the population dynamic consequences of habitat selection and reproductive success. This study describes the intersection of individual behavior and population regulation in the context of a new model of population regulation, site dependence, which is based on characteristics of breeding sites and behavior of individuals. I studied habitat distribution, age structure, reproductive output, and breeding site fidelity of Prothonotary Warblers (*Protonotaria citrea*) in two different bottomland hardwood forest habitats of the lower Roanoke River in North Carolina. Older males ($\geq$ 2 yr old) were equally common in cypress-gum swamps and mixed oak hardwood levee forest. Pairing success and success of first nests indicated that older males occupied the most suitable territories available in each habitat. Bird density was three times greater in swamps, and

birds nesting in swamps averaged greater clutch sizes and fledged more young per nest than birds in levees. Greater reproductive output was the result of greater fecundity because nest survival and predation pressure appeared equal in the two habitats. Annual return rates for plot immigrants vs. previous residents did not differ in swamps. In levees, newly arriving birds were less likely to return the following year than previous residents. Immigrants most likely occupied low quality sites and dispersed in an attempt to improve breeding site quality. Habitat-specific demography and density patterns of this study indicate ideal preemptive distribution. Variance in site quality, between and within habitats, and preemptive use of sites are consistent with theory of population regulation via site dependence.

Foraging behavior often reflects food availability. For example, in habitats where food availability is high, predators should move more slowly and attack prey more often than in habitats where food availability is low. I studied the foraging behavior of breeding Prothonotary Warblers in two habitat types to assess relative food availability and implications for habitat quality. The two habitats, levee and swamp forest, differ in hydrology, forest structure, and tree species composition. I quantified foraging behavior with focal animal sampling and continuous recording during foraging bouts. I measured two aspects of foraging behavior: 1) prey attacks per minute, using four attack types (glean, sally, hover, strike), and 2) number of movements per minute (foraging speed), using three types of movement (hop, short flight [≤ 1 m], long flight [>1 m]). Male warblers made significantly more prey attacks per minute in swamp forest than in levee forest; the same trend was evident in females. Foraging speed, however, was not different between habitats for males or females. Results indicate that foraging effort is similar in swamps and levees, but that warblers encounter more prey in swamps. Greater food availability may be related to greater reproductive success of warblers nesting in cypress-gum swamps than in coastal plain levee forest.

To my parents and siblings

and

To my first mentors in field biology,
especially Alan Hankin and Steve Reinert at the Lloyd Center for Environmental Studies,
and John Hagan and Brian Harrington at Manomet Bird Observatory

The whole of science is nothing more than a refinement of everyday thinking.

Einstein, *Physics and Reality*

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CHAPTER 1. NEST SUCCESS OF FOREST BIRDS IN BOTTOMLAND HARDWOOD FOREST: EFFECTS OF LEVEE WIDTH

Abstract

Nest survival often is lower at habitat edges than in habitat cores because of greater nest predation and parasitism near edges. I studied nest survival of breeding birds in bottomland hardwood forests of the lower Roanoke River, North Carolina. Bottomland hardwoods are naturally patchy landscapes that contain many different types of habitat edges (abrupt-gradual). Nesting success was monitored in two levee width classes: narrow bands of levee forest that were dominated by two edge types, and wide, continuous levee forest stands that have edges but most forest is relatively far from edge. Vegetation structure and composition were measured at nest sites and random sites to examine habitat selection. Nest success of Acadian Flycatchers and Prothonotary Warblers was similar in narrow and wide levees; nest success of Northern Cardinals was greater in narrow levees. Wide, continuous levees had a greater canopy height, denser shrub/midstory layer, and fewer large trees than narrow levees. Significant differences were observed in vegetation structure and composition at narrow vs. wide levee nest sites. These differences were similar to patterns found at random sites, however, and I conclude that birds were not selecting different habitat features depending on levee width. When nest sites were compared to random sites, variation in vegetation structure and composition indicated that nest placement was not random and that certain microhabitat features were selected. Results of my study indicate that edge effects are not universal, and that amount of contrast at edges may interact with landscape context to alter ecological processes, such as nest predation.

Introduction

Ecological processes often are altered at habitat edges in agricultural and silvicultural ecosystems. A particularly well documented example is elevated avian nest predation and nest parasitism rates near edges in forest patches within such landscapes in eastern North America (Robinson *et al.* 1995a). Explanations for increased nest predation rates at edges include: predators travel along edges while foraging; greater abundance of predators in edges; and greater species diversity of predators in edges (Askins *et al.* 1990, Hagan and Johnson 1992, Martin and Finch 1995). These explanations are not mutually exclusive, and other alternatives have been proposed (Marini *et al.* 1995). Nest parasitism rate often is higher near edges because Brown-headed Cowbirds (*Molothrus ater*) often are more abundant along edges than in core areas (Faaborg *et al.* 1995). Because habitat fragmentation increases amount of edge in a landscape, conservation biologists have focused efforts on describing the relationship between habitat fragmentation, changes in ecological processes, and declines of avian populations in North America (Robinson *et al.* 1995b, Sherry and Holmes 1995, Sherry and Holmes 1996).

Edge effects are not universal, however, and their relevance for avian population biology has been questioned (Paton 1994, Walters 1998). Ecological processes other than nest predation and parasitism (e.g., dispersal) may be paramount as causes of adverse impacts of habitat fragmentation, yet have received less research effort (Walters 1998). Other proximate factors associated with edge effects are poorly understood. For example, vegetation structure and composition at habitat edges vary substantially among landscapes. Suarez et al. (1997) found that predation rates were higher near abrupt, agricultural edges than near gradual, successional edges. They conclude that nest predation and nest parasitism are influenced by edge type.

Floodplains of major rivers are a complex mosaic of different forest cover types. The size, configuration, and number of forest patches are primarily determined by small changes in elevation and flooding regime. When a large number of forest patches are present in a landscape, a large amount of habitat edge exists in the transitional zone between forest stands (hereafter "stand edge"). Stand edges are "soft" or gradual edges, as opposed to "hard" or abrupt edges typically found in agricultural systems and even-aged silvicultural treatments. Floodplains also contain abrupt edges, namely those along the main river channel. Because they contain different types of edges, floodplains and bottomland hardwood forests are an ideal place to study effects of edge type on ecological processes.

Sallabanks *et al.* (2000) monitored bird populations and examined edge effects in the floodplain of the lower Roanoke River in North Carolina. Forests in this floodplain are composed of two primary cover types: levee forest and cypress-gum swamp. Sallabanks *et al.* (2000) conducted point counts at edge and interior locations in both levee forest and cypress-gum swamp, and found few edge effects. Overall, bird abundance was relatively high, and several rare species were observed during the breeding season (Sallabanks *et al.* 2000). Based on abundance and distribution of birds found on surveys, and on amount of available habitat, Sallabanks *et al*. (2000) suggested that the lower Roanoke bottomlands may be a regional source population for a number of species. Demographic information is required, however, to determine whether local populations indeed produce a surplus of individuals, and whether the lack of edge effects on abundance also applies to demography (Sallabanks *et al.* 2000). In a study using artificial nests in the lower Roanoke bottomlands, Saracco and Collazo (1999) found nest predation was greater at agricultural edges than at river edges or stand edges.

My study had three primary goals. First, effects of habitat edges on avian nesting success in levee forest were investigated. Levee forest occurs as a linear habitat adjacent to rivers, and I used natural variation in levee width to define edge and interior locations. Where levees are narrow, edge habitats predominate; narrow levees include both an abrupt edge at the river channel and a gradual, stand edge where the levee forest borders cypress-gum swamp forest. Where levees are wide, there is a core area far from either edge type. Second, differences in habitat features between narrow and wide levees are described, at both random sites and nest sites, to examine habitat selection relative to levee width and edges. Finally, nesting habitat is compared to habitat at random locations and overall patterns of habitat use in bottomland hardwood forest are described.

Methods and Study Site

Study site

This study was conducted in the natural levee forests of the lower Roanoke River floodplain, Martin and Bertie Counties, NC. Levee forest habitats of the lower Roanoke River generally occur in a linear band between the main river channel and backwater swamps. Levee width, which varies from several meters to over 1 km, is largely determined by historical patterns of erosion and sedimentation. Natural levees are formed adjacent to the main river channel when water levels overflow the riverbank. Soils of natural levees are generally sandy loams, formed by deposition of relatively heavy, coarse sediments close to the river channel. Lighter, finer sediments are carried further before settling; this process generates silty and clayey soils characteristic of backswamps.

Levee forests in this system are complex, dynamic assemblages, in which vegetation composition is largely determined by hydroperiod, erosion/sedimentation patterns, gap processes, and soil nutrient availability (Rice and Peet 1997). Narrow levees tend to have a longer hydroperiod because they are often closer to backswamps and sloughs, which are inundated for much of the year. Dominant canopy tree species in levee forest include *Fraxinus pennsylvanica*, *Lyquidambar styraciflua*, *Acer negundo*, *Acer rubrum*, *Ulmus americana*, and *Celtis laevigata*. Common in the shrub and midstory layers are *Asimina triloba*, *Ilex decidua*, *Fraxinus caroliniana*, and *Carpinus caroliniana*. Levee forests in this part of the lower Roanoke River basin are comparable to "Zone IV—Forests of Backwaters and Flats" (Christensen 2000) and "Coastal Plain Levee Forest, Brownwater Subtype" (Schafale and Weakley 1990).

Field Methods

To determine the effects of levee width on nest productivity, we established eight 25 ha study plots (4 each in narrow and wide levees). Levees that were 800 - 1500 m wide from river edge to backswamp or other habitats were categorized as "wide" levees. Wide levee study plots (500 x 500 m) were located roughly in the center of the levee forest patch so that the plot was at least 200 m from any edge habitat. Narrow levee plots (250 x 1000 m) were located in areas where levee width ranged from 200-300 m. These plots were less than 25 m from the river edge on one side and graded into backswamp habitats on the other. Narrow and wide levee plots were marked using a 25 x 25 m grid of plastic flags (50 cm high) to facilitate monitoring of nesting activities.

We searched for nests from late April to late June, 1994-1995. In addition, we conducted intensive studies of Acadian Flycatchers and Prothonotary Warblers in 1996, during which we

gathered supplemental nest data for these two species. Field technicians discovered nests by

noting behavioral cues that indicated nesting activity (e.g. adults carrying nest material or food),

and by systematically searching potential nest sites (Martin and Geupel 1993). Nests were

visited every 3-4 days to document nest success or failure. Number of eggs and young were

recorded during visits if possible. We determined the expected date of fledging using the

average length of incubation and nestling periods for each species. Nests were visited two days

before the expected fledging date to avoid disturbances that may cause premature fledging. A

nest was considered successful if at least one nestling survived to two days before the expected

fledging date.

To examine variation in nesting habitat structure and composition associated with levee

width, I measured several habitat variables. Habitat variables were classified before analyses

into 3 datasets: vegetation structure, vegetation composition, and nest microhabitat variables.

Structure variables included: (1) % canopy cover, (2) canopy height, (3) number of snags, (4)

number of plant species, and (5) stem counts using six size classes (shrubs, and stems <2.5 cm

dbh, 2.5 – 8 cm, 8.1 – 23 cm, 23.1 – 38, and >38 cm dbh). Shrubs were defined as stems 0.5 -

1.4 m tall. Shrubs, stems <2.5 cm dbh, and stems 2.5–8 cm dbh were tallied on circular sample

plots of 5 m radius. All other stem size classes, snags, and plant species richness were tallied on

circular sample plots of 11.3 m radius, centered on the same point as the 5 m plot. Canopy

height was measured using a clinometer and canopy cover was measured using a densiometer.

Vegetation composition variables were created using the stem totals for species found on circular

sample plots; that is, each vegetation species was treated as a variable whose value was equal to

the stem total for the sample plot. Nest microhabitat variables included: (1) nest height, (2) nest

tree height, (3) nest tree dbh, (4) % ground cover, and (5) distance of nest from main stem of nest tree (m).

Vegetation structure variables, vegetation composition variables, and nest microhabitat variables were measured at all nest sites with evidence of nesting. Vegetation structure and composition variables also were measured at random sites selected via systematic random sampling. Three parallel transects were established on each study plot. Because narrow levee study plots were rectangular and wide levee study plots were square, transect length and number of sample points were not the same in narrow and wide levees. On narrow levee study plots, transects were 900 m long with 4 stations at 300 m intervals. On wide levee plots, transects were 250 m long with 3 stations at 125 m intervals (Fig. 1.1). Vegetation was sampled at each station, and three sub-stations. Sub-stations were located 120 degrees from each other around the station center point, at a distance of 30 m from the center.

Statistical Methods

Nest success in narrow and wide levees was compared using the daily probability of nest survival (Mayfield 1961, 1975, Hensler and Nichols 1981). Nest attempts with uncertain outcomes were not included in analyses. Analyses of habitat data involved four comparisons of two groups: (1) random sites from narrow and wide levees, (2) nest sites from narrow and wide levees, (3) nest sites and random sites, and (4) successful and unsuccessful nests. Each of these comparisons was made using MANOVA to test differences in mean vectors between groups. When MANOVA indicated significant differences between groups, stepwise logistic regression was used to determine which variables were associated with those differences. MANOVA and stepwise logistic regression models were constructed for each set of variables, that is vegetation

structure, vegetation composition, and nest microhabitat variables. To further investigate patterns of nest placement, I determined what tree species/size class combination was used most often for nesting, and examined the density of such trees around the nest site and at random locations in the study plots.

<div align="center">Results</div>

Nest success and levee width

Field assistants discovered 149 nests of 24 species (Appendix 1). Sample size of Acadian Flycatchers, Prothonotary Warblers, and Northern Cardinals were adequate to test differences in nest survival between narrow and wide levees; other species did not have an adequate sample of nests for this test. Nest success of Acadian Flycatchers was equal on narrow and wide levee plots. Six (19%) nests were successful on narrow levees, and nine (23%) on wide levees; daily probability of nest survival was 0.94 and 0.95 in narrow and wide levees, respectively (Table 1.1). Nest success was higher for Prothonotary Warblers but, similar to the flycatcher, did not vary with levee width. Twenty-four (36%) and 17 (34%) nests were successful in narrow and wide levees, respectively, and daily probability of nest survival was about 0.96 in each width category (Table 1.1). Northern Cardinals had greater nest success in narrow levees than in wide levees. Daily probability of nest survival was 0.97 and 0.87 for narrow and wide levees, respectively (Table 1.1).

Random sampling of vegetation in narrow and wide levee

Vegetation structure at random points varied with levee width (Wilks' $\Lambda = 0.71$, $F = 13.25$, df = [10, 321], $P < .0001$). Stepwise logistic regression indicated that canopy height and four stem size classes distinguished narrow and wide levees (Table 1.2). Relative to narrow levees, wide levees had a taller canopy (Table 1.3), greater density of shrubs, and greater density of trees < 2.5 cm dbh (Fig. 1.2). Wide levees also had a lower density of trees 8-23 and >38 cm dbh than narrow levees (Fig. 1.2). Wide levees thus had a more developed shrub/midstory layer and a lower density of canopy trees than narrow levees. Canopy closure was nearly complete in both levee width classes, averaging about 95% (Table 1.3).

Vegetation composition at random sites also varied with levee width (Wilks' $\Lambda = 0.44$, $F = 11.33$, df = [34, 101], $P < 0.0001$). Stepwise logistic regression indicated that densities of seven tree species distinguished narrow and wide levees (Table 1.4). These species included four found primarily in the canopy layer (*C. laevigata*, *T. distichum*, *P. deltoides*, and *Q. michauxii*), and three found primarily in the shrub/midstory layer (*I. decidua*, *Crataegus*, and *A. triloba*; Fig. 1.3). Overall, the magnitude of variation in species composition was more substantial in the shrub/midstory layer than in the canopy: *A. triloba* was an overwhelming midstory dominant on wide levees (Fig. 1.3).

Vegetation near nest sites in narrow and wide levee

Vegetation structure varied with levee width at nest sites of all three species (Table 1.5a). Patterns of vegetation structure found at nest sites reflected patterns found at random sites. Acadian Flycatcher and Northern Cardinal nest sites contained fewer trees <2.5 cm dbh on

narrow levees than on wide levees (Table 1.6, Fig. 1.4, Fig. 1.6). Prothonotary Warbler nest sites contained fewer shrubs and more trees 8 – 23 cm dbh on narrow levees (Table 1.6, Fig. 1.5).

Nest sites in narrow and wide levees also had different vegetation composition (Table 1.5b). Stepwise logistic regression indicated that *A. triloba* was more abundant on wide levees than narrow at nest sites of Acadian Flycatchers, Prothonotary Warblers, and Northern Cardinals (Table 1.7). Furthermore, there was less *I. decidua* at Prothonotary Warbler nest sites in wide levees than narrow. Vegetation composition at nest sites thus was similar to composition at random sites.

Nest microhabitat variables did not differ in narrow and wide levee forest (Table 1.5c).

Nest vs. random sites

When vegetation structure at nests was compared to vegetation structure at random sites from the systematic sample, significant differences were found for each species (Table 1.8). Acadian Flycatchers placed nests in areas with less canopy cover, fewer trees 2.5 – 8 cm dbh, and fewer trees > 38 cm dbh than found at random sites (Table 1.9, Fig. 1.7). Acadian Flycatchers used laurel oak (*Q. laurifolia* [23-38 cm dbh]) most often for nesting (27% of all nests). Laurel Oaks of this size class were more common around nest sites (12.4 per ha [± 18.4 SD]) than at random locations (7.8 per ha [± 18.6 SD]; t = -2.33, df = 411, *P* = 0.02). Prothonotary Warbler nest sites had less canopy cover and greater snag density than random sites (Table 1.9, Fig. 1.8). Northern Cardinal nest sites also had less canopy cover, but a greater stem density in the 2.5 – 8 cm dbh class than random points (Table 1.9, Fig. 1.9). Most nests of Northern Cardinals (27%) were placed in deciduous holly (2.5-8 cm dbh). Deciduous holly

stems of this size class were less common around nest sites (19.5 per ha [± 58.9 SD]) than at random locations (160.6 per ha [± 317.0 SD]; t = 6.14, df = 73.9, $P < 0.0001$).

Successful vs. Failed Nests

No significant differences were found between sites of successful nests and failed nests among vegetation structure, vegetation composition, or nest microhabitat variables (Table 1.10).

<div align="center">Discussion</div>

Edge effects

Narrow levees along the lower Roanoke River were impacted by two types of edges. If nest predation was universally higher at habitat edges, lower nesting success would be expected in narrow levees. Yet nesting success at this edge-dominated habitat was equal to nesting success at interior locations for two of three species and, contrary to expectations, nesting success of a third species (Northern Cardinal) was greater in narrow levees than in wide. These results support the notion that different edge types do not necessarily produce similar changes in ecological processes (Suarez *et al.* 1997, Walters 1998, Saracco and Collazo 1999).

It may be unjustified to assume that all species will have lower nesting success in edge habitats. Species with an evolutionary history of nesting on edges may have adaptations to avoid higher predation pressures relative to interior locations. Northern Cardinals often nest in shrubs and thickets (Ehrlich *et al.* 1988, Sibley 2000), and therefore may be considered edge species. This may be why Northern Cardinals had higher nest success in narrow levees, and why this species may not provide a good test of edge effects in this system.

In an artificial nest experiment conducted in some of the same forest stands as my study, Saracco and Collazo (1999) observed greater nest predation at forest-farm edges than at river-levee or levee-swamp stand edges. Forest-farm edges studied by Saracco and Collazo (1999) were abrupt edges that occurred at the border of levee forest and agricultural land, often more than 500 m from the river channel. The combined results of Saracco and Collazo (1999) and my study suggest that nest predation is influenced not only by amount of contrast at ecotones, but also by landscape context or matrix effects (Donovan *et al.* 1997). Highest predation rate was observed at abrupt, agricultural edges, and not at abrupt, river edges or gradual, levee-swamp stand edges (Saracco and Collazo 1999, this study).

Several studies have examined relationships between amount of contrast at edges, landscape context, and avian nesting success. Evidence for contrast effects has been inconclusive (Paton 1994). Nest predation has been greater at abrupt edges (Sargent *et al.* 1998, Suarez *et al.* 1997), greater at gradual edges (Ratti and Reese 1988, Fenske-Crawford and Niemi 1997), or unaffected by edge type (Yahner *et al.* 1989). Similar to contrast effects, landscape context is a subject in need of further research. Donovan et al. (1997) observed increased nest predation at edges in moderately and highly fragmented landscapes, but not in unfragmented landscapes. Future studies of edge effects should focus on interactions between amount of contrast (abrupt-gradual) and landscape context (e.g. agricultural, rural, suburban, silvicultural). If contrast and landscape effects can be separated, conflicting evidence about edge effects may be reconciled.

Nesting habitat selection

Vegetation features of narrow and wide levees were different in many ways, including both structural and compositional variation. A remarkable structural difference was observed in shrub/midstory vegetation: stem density in smaller size classes was higher on wide levees, with one species, *A. triloba*, accounting for most of the difference. Variation in species composition, and indirectly vegetation structure, may be the result of variation in hydroperiod between narrow and wide levees. Wide levees are often slightly higher (in most cases by mere centimeters), which may result in a substantially shorter duration of flooding throughout the annual cycle. Narrow levees had a significantly greater density of *T. distichum*, a strong indication of saturated soils given the water tolerance of this species. Hydrologic regime and edaphic conditions thus resulted in significant differences in available nesting habitat on narrow and wide levees.

Variation in habitat selected for nesting was minimal, and largely reflected variation in available habitat. For the three species considered, habitat features that distinguished nest sites in narrow and wide levees also distinguished random points, e.g. greater sapling (< 2.5 cm dbh) density in wide levees (Tables 2 and 6). Because comparison of nest sites between levee width classes reveals similar patterns to a comparison of random points, there is little evidence that birds were altering habitat selection behavior depending on levee width. Birds selected certain habitat features when placing nests (see below), but those habitat features were not related to levee width.

Systematic random samples of habitat structure and composition provided insight about habitat preferences. Habitat features that were preferred by birds appeared related to nesting ecology, and possibly to foraging ecology. For example, Prothonotary Warbler nest sites contained more snags and less canopy cover than systematic random points; these differences

clearly represent habitat selection by this cavity nesting species (Table 1.10). Acadian Flycatcher nest sites had a more open midstory and a more open canopy than random locations. Flycatchers may have greater hunting success in areas with a more open midstory because flying insects are more visible in open areas, and possibly more active as well. The immediate area around Acadian Flycatcher nests also contained a greater density of the tree species/size classes preferred for nesting (laurel oaks, 23-38 cm dbh) than random sites.

Edges have been characterized as "ecological traps," and indeed there is remarkable evidence of reduced productivity of nesting birds on edges in some landscapes (e.g. agricultural and suburban). Recent studies of edge type suggest that ecological processes are not the same at all types of edges, however, and proximate mechanisms that produce greater predation pressure, for example, are not well known. Furthermore, it is clear that unfragmented and naturally fragmented landscapes do not show the same edge effects as human-fragmented landscapes (Donovan *et al.* 1997, this study). A better understanding of mechanisms responsible for edge effects may depend on successful measurement of effects related to edge contrast and landscape context.

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Table 1.1. Nest survival for three species in narrow and wide levee locations. "Nest exposure days" is the total number of days that active nests were monitored.

Location	No. nests	No. successful	Nest exposure days	Daily probability of nest survival	Nest survival variance	95% confidence interval[a]	Mayfield nest success estimate[b]	P^c
Acadian Flycatcher								
NARROW	25	6	343.0	0.945	1.525×10^{-4}	(0.920, 0.969)	0.19	0.3821
WIDE	30	9	415.5	0.949	1.155×10^{-4}	(0.928, 0.971)	0.22	
Prothonotary Warbler								
NARROW	41	24	493.0	0.966	6.753×10^{-5}	(0.950, 0.982)	0.43	0.3300
WIDE	33	17	399.0	0.959	9.647×10^{-5}	(0.941, 0.980)	0.37	
Northern Cardinal								

NARROW	12	8	152.0	0.974	1.697×10^{-4}	(0.948, 0.999)	0.57	<0.0001
WIDE	7	1	46.0	0.868	2.516×10^{-4}	(0.838, 0.899)	0.05	

[a] confidence interval for daily probability of nest survival

[b] (daily prob. of nest survival)^k ; k = # days in nest cycle = 29 (Acadian Flycatcher), 24 (Prothonotary Warbler), or 21 (Northern Cardinal)

[c] probability of the observed difference in nest survival between narrow and wide locations based on Hensler and Nichols (1981)

Table 1.2. Vegetation structure at random sites (n = 336) varied between narrow and wide levees. Stepwise logistic regression indicated that 5 of 10 vegetation structure variables accounted for significant variation between levee width classes (parameter estimates reflect probability that levee width class is "Narrow"). Stem counts were transformed using square root; canopy height using natural logarithm. Only significant variables are shown.

Variable	Parameter	SE	χ^2	P
Canopy height	-2.439	0.823	8.786	0.0030
Shrubs	-0.430	0.149	8.362	0.0380
Trees < 2.5 cm dbh	-0.462	0.145	10.150	0.0014
Trees 8-23 cm dbh	1.252	0.321	15.233	< 0.0001
Trees > 38 cm dbh	0.642	0.296	4.689	0.0303

Table 1.3. Selected vegetation structure variables for narrow and wide levees. Mean values (± SE) are shown for four samples: random sites, Acadian Flycatcher nests, Prothonotary Warbler nests, and Northern Cardinal nests.

	Narrow levee	Wide levee
Canopy height (m)		
Random sites[a]	30.2 ± 0.3	32.2 ± 0.7
Acadian Flycatcher nest[b]	30.2 ± 0.6	29.6 ± 0.8
Prothonotary Warbler nest[c]	29.9 ± 0.7	29.6 ± 0.9
Northern Cardinal nest[d]	28.6 ± 1.5	29.8 ± 2.3
Canopy cover		
Random sites	0.953 ± 0.002	0.950 ± 0.002
Acadian Flycatcher nest	0.941 ± 0.009	0.929 ± 0.008
Prothonotary Warbler nest	0.936 ± 0.008	0.941 ± 0.005
Northern Cardinal nest	0.925 ± 0.015	0.939 ± 0.010
Snag density (no. snags/11.3 m radius plot)		
Random sites	1.3 ± 0.1	1.1 ± 0.1

Acadian Flycatcher nest	1.0 ± 0.2	1.2 ± 0.2
Prothonotary Warbler nest	1.9 ± 0.2	2.0 ± 0.3
Northern Cardinal nest	1.3 ± 0.3	0.8 ± 0.3

Tree species richness (no. species/11.3 m radius plot)

Random sites	8.1 ± 0.1	8.0 ± 0.2
Acadian Flycatcher nest	8.1 ± 0.3	8.2 ± 0.3
Prothonotary Warbler nest	7.9 ± 0.3	8.2 ± 0.4
Northern Cardinal nest	7.8 ± 0.4	7.9 ± 0.5

[a] sample size for random sites: 192 narrow, 144 wide

[b] " " " Acadian Flycatcher nests: 37 narrow, 40 wide

[c] " " " Prothonotary Warbler nests: 55 narrow, 33 wide

[d] " " " Northern Cardinal nests: 15 narrow, 11 wide

Table 1.4. Vegetation composition at 336 random sites varied between levee width classes. Variables (i.e. tree species) selected in a stepwise logistic regression model of levee width are shown. Only significant variables are shown. Parameter estimates reflect probability that levee width category is "Narrow." Vegetation composition data were transformed using square root.

Variable	Parameter	SE	χ^2	P
Taxodium distichum	1.617	0.622	6.760	0.0093
Ilex deciduas	1.170	0.269	18.934	< 0.0001
Populus deltoids	-1.445	0.726	3.960	0.0466
Celtis laevigata	0.801	0.283	8.031	0.0046
Crataegus sp.	2.397	1.141	4.411	0.0357
Asimina triloba	-1.099	0.189	33.957	< 0.0001
Quercus michauxii	-1.379	0.659	4.369	0.0366

Table 1.5. Results of MANOVA analyses comparing nest sites on narrow and wide levees. Each line in the table represents a separate MANOVA to test differences between nest sites on narrow and wide levees using vegetation structure, vegetation composition, or nest microhabitat variables.

	Wilks' Λ	F	df	P
(a) Vegetation structure variables				
Acadian Flycatcher	0.674	3.156	10,65	0.0024
Prothonotary Warbler	0.678	3.564	10,75	0.0007
Northern Cardinal	0.286	3.748	10,15	0.0108
(b) Vegetation composition variables				
Acadian Flycatcher	0.476	1.788	29,47	0.0383
Prothonotary Warbler	0.415	2.686	30,57	0.0007
Northern Cardinal	0.003	47.466	22,3	0.0043
(c) Nest microhabitat variables				
Acadian Flycatcher[a]	0.923	0.791	5,47	0.5638
Prothonotary Warbler[b]	0.879	1.519	4,44	0.2146
Northern Cardinal[c]	0.987	0.091	3,19	0.9670

[a] nest ht., nest tree ht., nest tree dbh, ground cover, distance to stem

[b] nest ht., nest tree ht., nest tree dbh, ground cover

[c] nest ht., nest tree ht., nest tree dbh

Table 1.6. Vegetation structure at nest sites varied with levee width. Stepwise logistic regression models of levee width ("Narrow" vs. "Wide") indicated which structural variables accounted for variation between nest sites on narrow and wide levees. Only significant variables are shown. Parameter estimates indicate probability that levee width category is "Narrow." Stem counts were transformed using square root. These results are similar to those for random sites.

Variable	Parameter	SE	χ^2	P
Acadian Flycatcher (n = 76)				
Trees < 2.5 cm dbh	-0.982	0.274	12.844	0.0003
Prothonotary Warbler (n = 86)				
Shrubs	-0.800	0.243	10.817	0.0010
Trees 8-23 cm dbh	1.181	0.450	6.886	0.0087
Northern Cardinal (n = 26)				
Trees < 2.5 cm dbh	-2.482	1.042	5.672	0.0172

Table 1.7. Vegetation composition at nest sites varied with levee width. Results of stepwise logistic regression analysis of levee width ("Narrow" vs. "Wide") are shown. Parameter estimates indicate probability that levee width category is "Narrow." Only significant variables are shown. Vegetation composition data were transformed using square root. These results are similar to those for random sites.

Variable	Parameter	SE	χ^2	P
Acadian Flycatcher (n = 77)				
Asimina triloba	-1.332	0.368	13.069	0.0003
Prothonotary Warbler (n = 88)				
Asimina triloba	-0.617	0.188	10.753	0.0010
Ilex decidua	1.302	0.444	8.591	0.0034
Northern Cardinal (n = 26)				
Asimina triloba	-2.028	0.804	6.354	0.0117

Table 1.8. Results of MANOVA analyses testing differences in vegetation structure at nest and random sites. Each line in the table represents a separate MANOVA using 10 vegetation structure variables to test differences in mean vectors for nest and random sites.

	Wilks' Λ	F	df	P
Vegetation structure variables				
Acadian Flycatcher	0.943	2.422	10,397	0.0084
Prothonotary Warbler	0.898	4.621	10,407	< 0.0001
Northern Cardinal	0.925	2.811	10,347	0.0023

Table 1.9. Vegetation structure at nest sites was significantly different from structure at random sites. Stepwise logistic regression analysis using 10 vegetation structure variables indicated which variables best described differences between nest sites and random sites for each species. Parameter estimates indicate probability that observations are nest sites. Only significant variables are shown (data were transformed using square root [stem counts] or angular transformation [% canopy cover, % ground cover]).

Variable	Parameter	SE	χ^2	P
Acadian Flycatcher (n = 408)				
Canopy cover	-3.539	1.632	4.704	0.0301
Trees 2.5 - 8.0 cm dbh	-0.379	0.137	7.685	0.0056
Trees > 38 cm dbh	-0.658	0.240	7.528	0.0061
Prothonotary Warbler (n = 418)				
Canopy cover	-6.059	1.680	13.009	0.0003
Snags	1.117	0.253	19.539	< 0.0001
Northern Cardinal (n = 358)				
Canopy cover	-8.540	2.671	10.226	0.0014
Trees 2.5 - 8.0 cm dbh	0.595	0.184	10.477	0.0012

Table 1.10. Results of MANOVA analyses that compared successful to unsuccessful nest sites. Each line in the table represents a separate MANOVA using vegetation structure, vegetation composition, or nest microhabitat variables to test differences in mean vectors for successful and unsuccessful nests.

	Wilks' Λ	F	df	P
(a) Vegetation structure variables				
Acadian Flycatcher	0.802	1.060	10,43	0.4104
Prothonotary Warbler	0.890	0.701	10,57	0.7163
Northern Cardinal	0.527	0.909	10,10	0.5654
(b) Vegetation composition variables				
Acadian Flycatcher	0.582	0.676	28,26	0.8512
Prothonotary Warbler	0.616	0.860	29,40	0.6595
Northern Cardinal[a]	-	-	-	-
(c) Nest Microhabitat variables				
Acadian Flycatcher	0.804	1.564	5,32	0.2005
Prothonotary Warbler	0.987	0.243	3,56	0.8684
Northern Cardinal	0.953	0.234	3,14	0.8736

[a] sample size inadequate

42
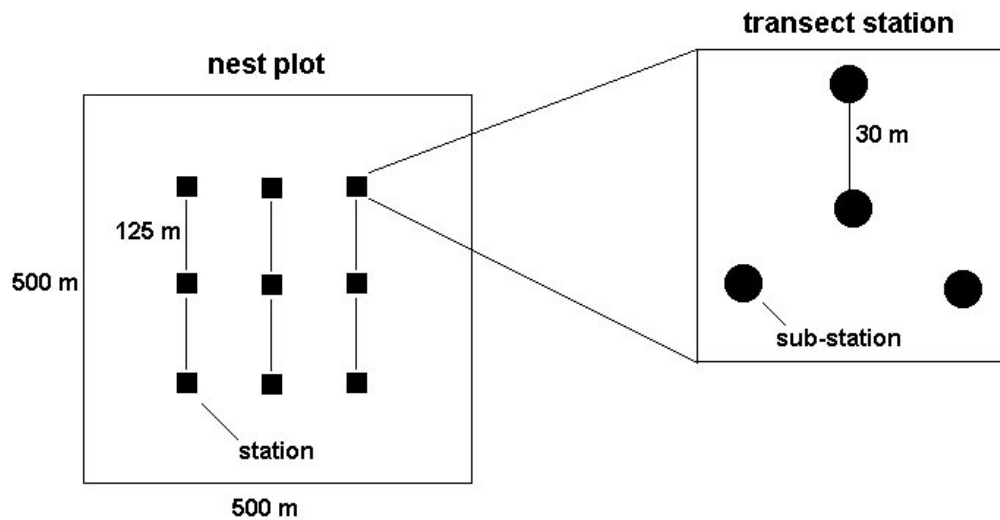
Figure 1.1. Schematic representation of study plot and transects used to sample vegetation.

Shown is a wide levee nest plot; plot shape and configuration of transect stations is different for

narrow levee nest plots (see Methods).

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Random sites
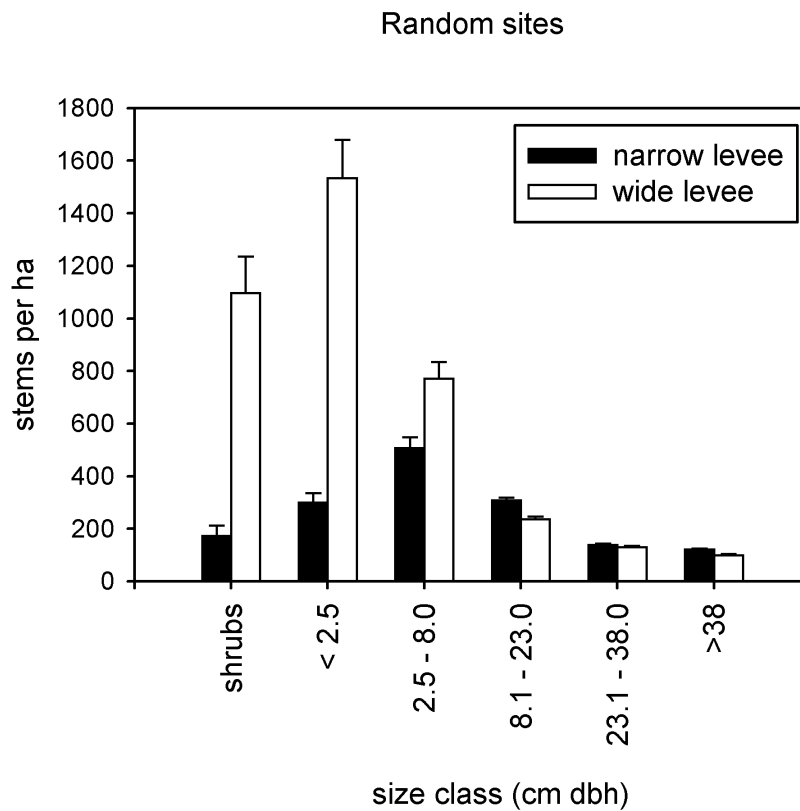
Figure 1.2. Stem density in six size classes based on systematic random sampling of narrow and wide levee nest plots.
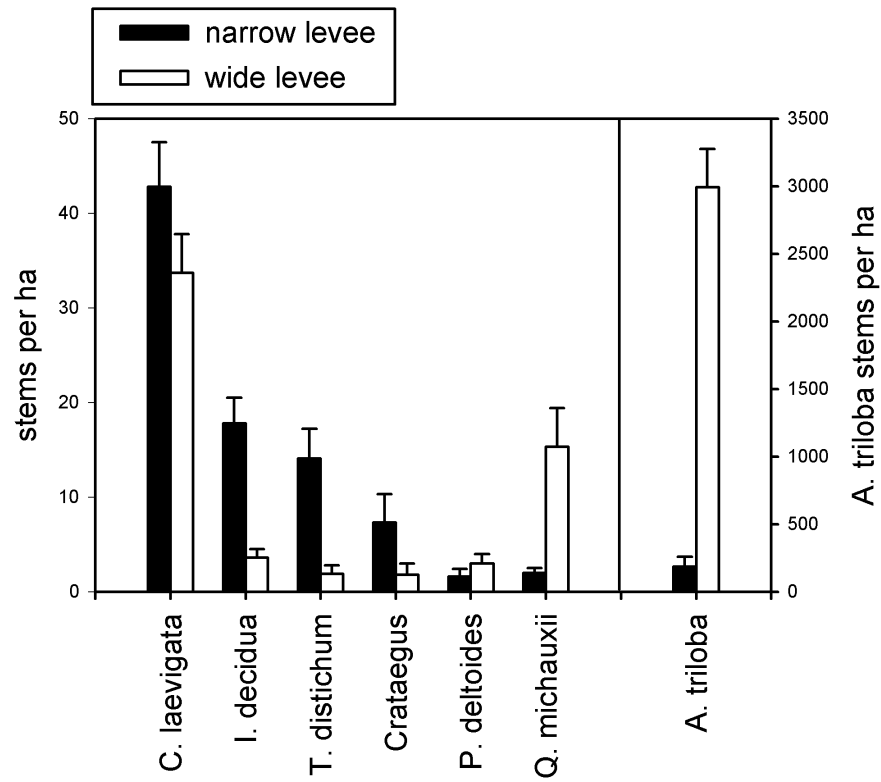
Figure 1.3. Vegetation composition based on a systematic random sampling of narrow and wide levee nest plots.
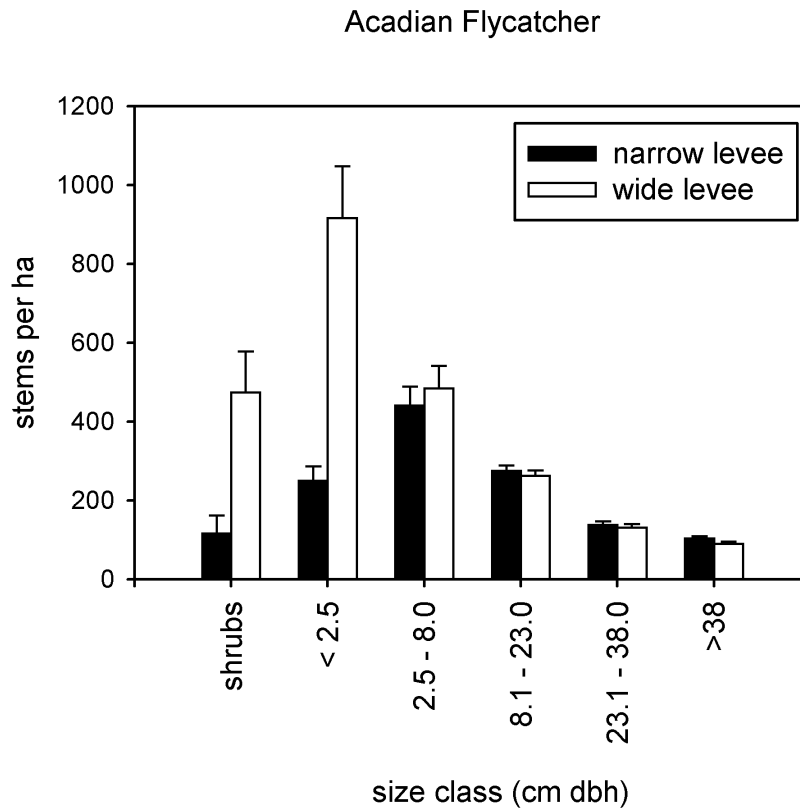
Figure 1.4. Stem density in six size classes at Acadian Flycatcher nests.
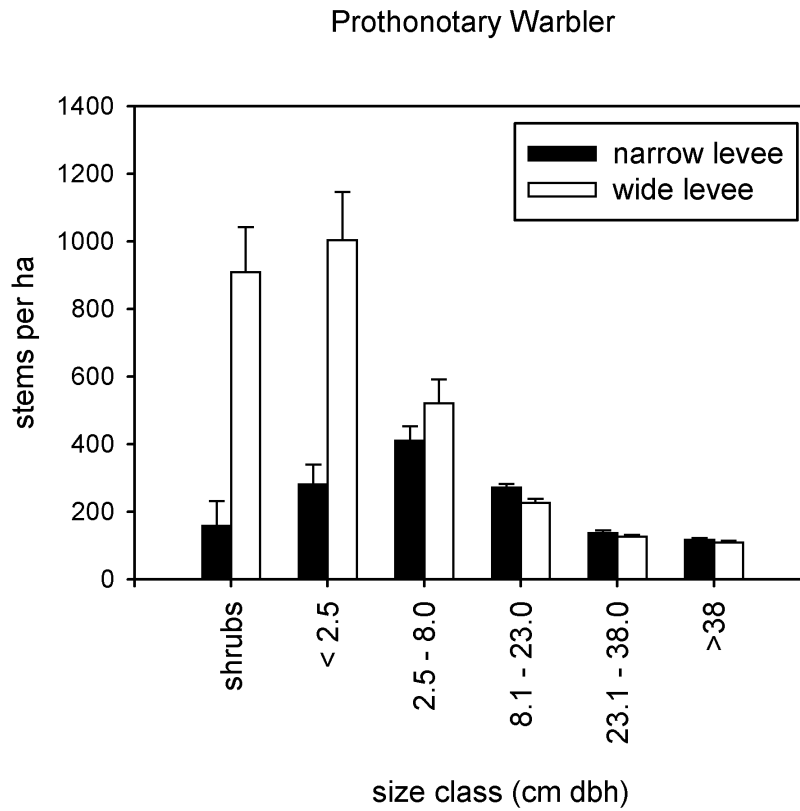
Figure 1.5. Stem density in six size classes at Prothonotary Warbler nests.
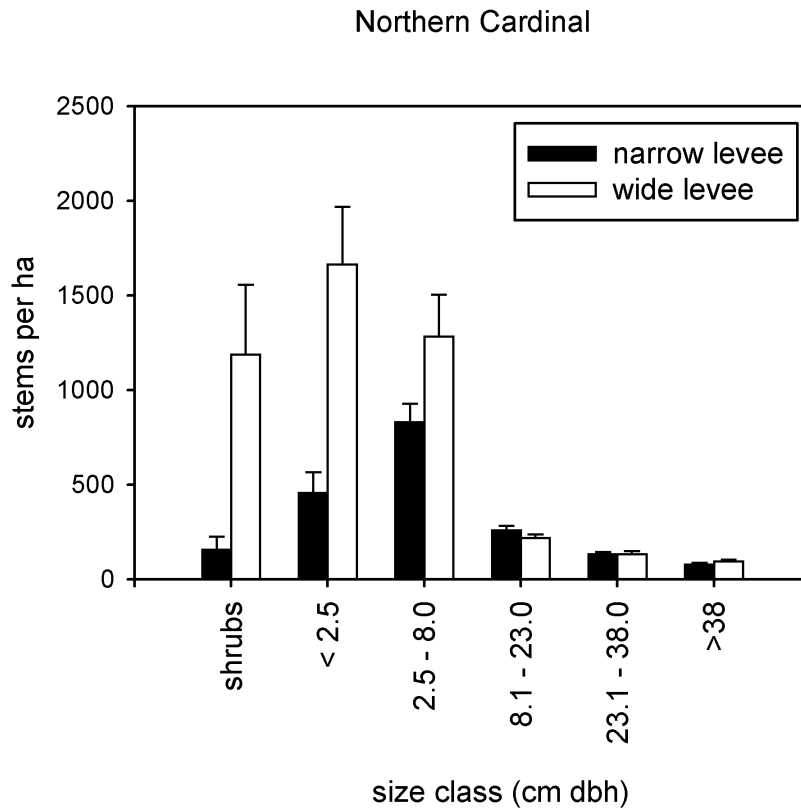
Figure 1.6. Stem density in six size classes at Northern Cardinal nests.
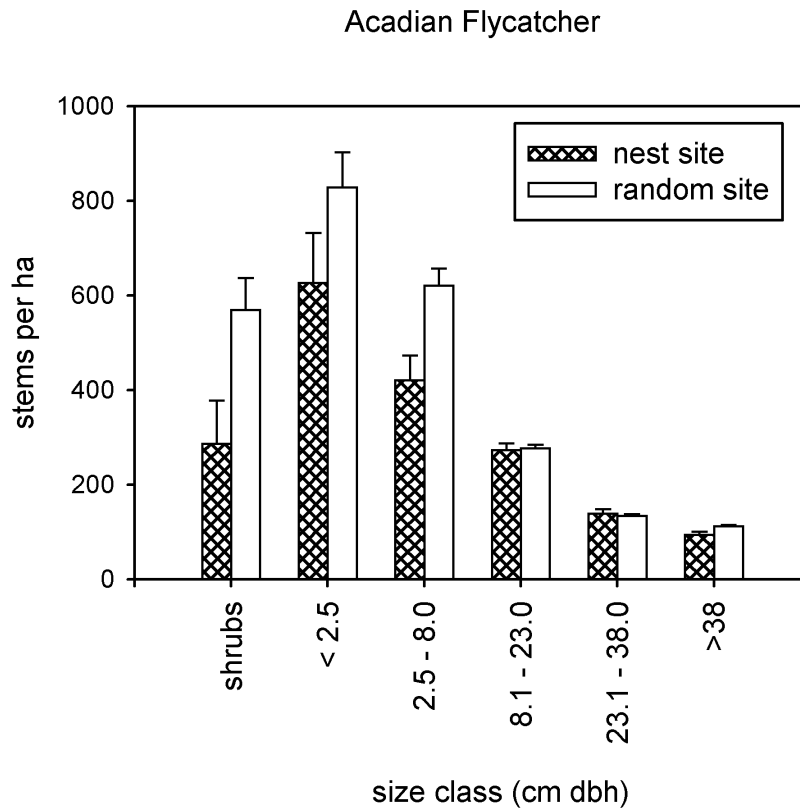
Figure 1.7. Stem density at Acadian Flycatcher nest sites and at systematic random points.
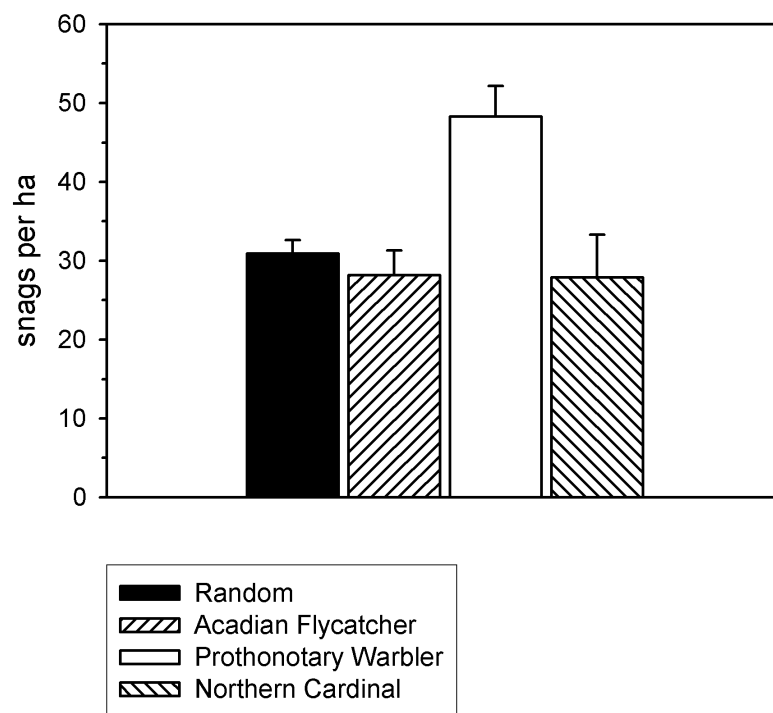
Figure 1.8. Snag density at systematic random points and nest sites of Acadian Flycatchers, Prothonotary Warblers, and Northern Cardinals.
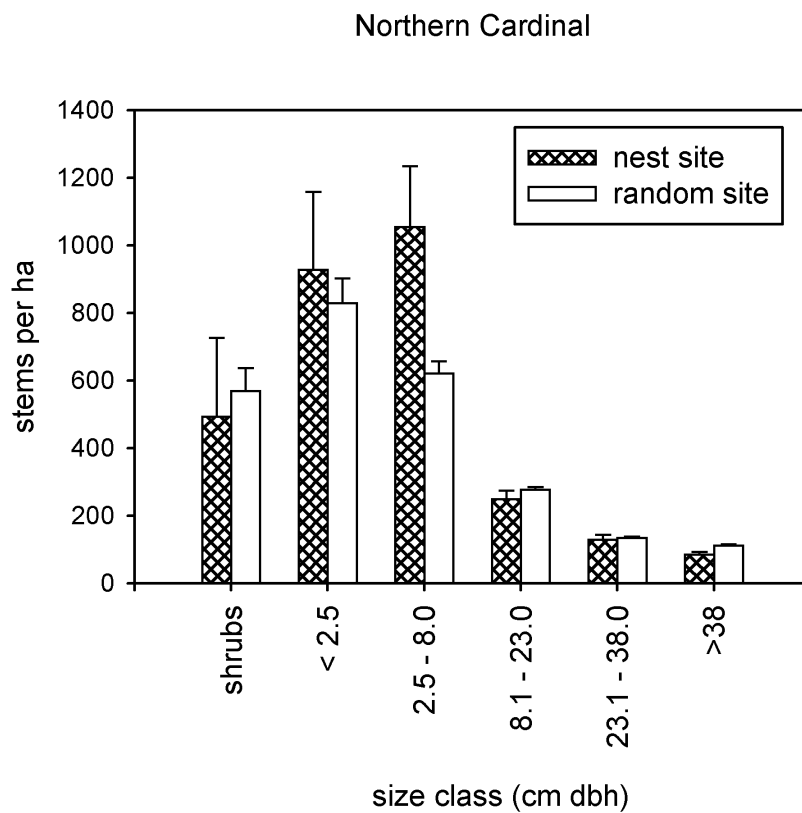
Figure 1.9. Stem density found at Northern Cardinal nests and systematic random points.

Appendix 1. Nest fate summary for species with small sample size.

		Nest fate			
	Location	Failure	Success	Uncertain[a]	Total
Wood Duck	Narrow	0	0	0	0
(Aix sponsa)	Wide	0	1	0	1
Red-shouldered Hawk	Narrow	0	0	0	0
(Buteo lineatus)	Wide	0	1	0	1
Wild Turkey	Narrow	2	0	0	2
(Meleagris gallopavo)	Wide	0	1	0	1
Yellow-billed Cuckoo	Narrow	1	0	0	1
(Coccyzus americanus)	Wide	0	0	0	0
Ruby-throated Hummingbird	Narrow	0	0	0	0
(Archilochus colubris)	Wide	1	0	0	1
Red-bellied Woodpecker	Narrow	1	3	1	5
(Melanerpes carolinus)	Wide	1	3	1	5
Downy Woodpecker	Narrow	0	3	0	3
(Picoides pubescens)	Wide	0	3	4	7
Pileated Woodpecker	Narrow	0	0	1	1

(Dryocopus pileatus)	Wide	0	1	0	1
Great Crested Flycatcher	Narrow	0	0	2	2
(Myiarchus crinitus)	Wide	0	0	0	0
White-eyed Vireo	Narrow	0	0	0	0
(Vireo griseus)	Wide	0	2	0	2
Red-eyed Vireo	Narrow	0	0	3	3
(Vireo olivaceus)	Wide	0	2	1	3
Carolina Chickadee	Narrow	0	1	1	2
(Poecile carolinensis)	Wide	1	1	0	2
Tufted Titmouse	Narrow	0	0	0	0
(Baelophus bicolor)	Wide	0	1	1	2
Carolina Wren	Narrow	2	1	4	7
(Thryothorus ludovicianus)	Wide	3	3	0	6
Blue-gray Gnatcatcher	Narrow	0	0	1	1
(Polioptila caerulea)	Wide	0	0	0	0
Wood Thrush	Narrow	4	1	5	10
(Hylocichla mustelina)	Wide	3	0	0	3
American Redstart	Narrow	0	0	2	2

(Setophaga ruticilla)	Wide	1	0	3	4
Swainson's Warbler	Narrow	0	1	0	1
(Limnothlypis	Wide	0	0	1	1
swainsonii)					
Kentucky Warbler	Narrow	0	0	0	0
(Oporonis formosus)	Wide	0	0	2	2
Summer Tanager	Narrow	0	0	1	1
(Piranga rubra)	Wide	1	0	0	1
Scarlet Tanager	Narrow	0	1	0	1
(Piranga olivacea)	Wide	1	0	1	2
Total		22	30	35	87

[a] includes nests that failed before eggs were laid and nests with unknown fates due to insufficient monitoring

CHAPTER 2. HABITAT-SPECIFIC DEMOGRAPHY, BREEDING SITE FIDELITY, AND POTENTIAL POPULATION REGULATION IN A TERRITORIAL, MIGRATORY PASSERINE (*PROTONOTARIA CITREA*)

Abstract

Bird populations are remarkably constant over time relative to other taxa, implying strong regulation. Avian population ecologists, however, have not studied regulatory mechanisms as often as seasonal limiting factors. Conversely, avian behavioral ecologists seldom emphasize the population dynamic consequences of habitat selection and reproductive success. This study describes the intersection of individual behavior and population regulation in the context of a new model of population regulation, site dependence, which is based on characteristics of breeding sites and behavior of individuals. I studied habitat distribution, age structure, reproductive output, and breeding site fidelity of Prothonotary Warblers (*Protonotaria citrea*) in two different bottomland hardwood forest habitats of the lower Roanoke River in North Carolina. Three plots were established in each habitat type and monitored during 1995-1997. Older males ($\geq$ 2 yr old) were equally common in cypress-gum swamps and mixed oak hardwood levee forest. Pairing success and success of first nests indicated that older males occupied the most suitable territories available in each habitat. Bird density was three times greater in swamps, and birds nesting in swamps averaged greater clutch sizes and fledged more young per nest than birds in levees. Greater reproductive output was the result of greater fecundity because nest survival and predation pressure appeared equal in the two habitats. Annual return rates for plot immigrants vs. previous residents did not differ in swamps. In levees, newly arriving birds were less likely to return the following year than previous residents. Immigrants most likely occupied low quality sites and dispersed in an attempt to improve breeding site quality. Habitat-specific demography and density patterns of this study indicate

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ideal preemptive distribution. Variance in site quality, between and within habitats, and preemptive use of sites are consistent with theory of population regulation via site dependence.

Introduction

Studies of bird evolution focus on changes in behavior, physiology, and life-history in response to natural selection, but often ignore population dynamics. Behavior, physiology, and natural history, however, are the phenomena that determine birth, death, and dispersal rates and therefore population dynamics (Murdoch 1994). Whereas behavioral ecologists focus on proximate and ultimate causation, population biologists often study demographic consequences of environmental or biological changes with little consideration for the behavioral mechanisms that may underlie changes in vital rates (Hassell and May 1985). Yet studies that link the behavior of individuals to population dynamics may be the best way to discover important mechanisms in population ecology (Pulliam *et al.* 1992, Murdoch 1994, Goss-Custard *et al.* 1995, Gordon 1997, Sutherland 1996). This study describes the habitat selection behavior, demography, and breeding site fidelity patterns that may influence population fluctuations in a migratory passerine, the Prothonotary Warbler (*Protonotaria citrea*).

Abundance and distribution among habitats are the result of behavioral responses to spatial and temporal variation in resources. There are several theoretical models of habitat distribution, the best known of which is the ideal free distribution (Fretwell and Lucas 1970, Fretwell 1972). This model assumes that available habitats vary in suitability (Block and Brennen 1993) even when empty, and that there is a negative relationship between habitat suitability and density of residents. The model also assumes that individuals have complete ("ideal") knowledge of all available habitats and that they are "free" to move and occupy any

habitat. Under these assumptions, ideal free distribution results in unequal densities among habitats, yet equal fitness for all individuals in the population. Equal fitness is the result of declines in per capita resources with increasing density. Brown (1969a, 1969b), Orians (1969), Parker (1970) and Royama (1970) independently developed similar ideas about habitat distribution, but did not produce a general theory of habitat selection.

Another theoretical model of habitat distribution with implications for population dynamics is the source/sink model of Pulliam (1988). Source habitats are those that produce a surplus of individuals in excess of mortality, whereas sink habitats are not productive enough to balance mortality; sinks remain extant only through immigration from sources. Pulliam and Danielson (1991) described habitat occupancy patterns in a source/sink scenario and developed an alternative to ideal free distribution, ideal preemptive distribution, which is qualitatively similar to Fretwell's (1972) ideal despotic. Ideal preemptive selection occurs when individuals choose the best unoccupied site and thereby prevent others from using resources associated with that site.   Ideal preemptive models, unlike ideal free models, predict unequal average reproductive success between habitats (i.e., per capita resources are not affected by increasing density).

Historically, theoretical models of population dynamics have been more contentious than habitat distribution models. Nicholson (1933, Nicholson and Bailey 1935) insisted that density dependent factors must be responsible for relative stability of populations in nature. Andrewartha and Birch (1954), however, concluded that all factors are likely density-dependent, including for example weather-induced mortality, and therefore there is no need for special emphasis on density-dependence vs. density-independence. The most likely explanation for apparent regulation in natural populations is short periods of time with a positive intrinsic rate of

growth (Andrewartha and Birch 1954). Recent theory and empirical evidence of regulation suggest that both schools of thought are partially correct (Strong 1986, Chesson and Case 1986, Murdoch 1994). Density dependent regulation is generally accepted as a requirement for population stabilization, yet local stochastic events and asynchronous subpopulations may stabilize populations (Cappuccino 1995, Murdoch 1994). One issue that remains is to discover the mechanisms of population regulation.

Population limitation of migratory passerines has recently received considerable attention (Sherry and Holmes 1993, Sherry and Holmes 1996, Rappole and McDonald 1994, Maurer and Villard 1996). Debate has focused on whether populations that breed in Nearctic terrestrial habitats and migrate to Neotropical habitats are limited (*i.e.* constrained below an upper limit or "ceiling") during the temperate breeding or tropical nonbreeding season. "Summer vs. winter limitation" debate is the result of evidence that populations of some Nearctic-Neotropical migrant birds are declining (Terborgh 1989, Robbins *et al.* 1989, James *et al.* 1992). The emerging consensus, based largely on empirical observations, is that Nearctic-Neotropical migrants may be limited at all phases of the annual cycle—breeding, migratory, and "wintering" (Sherry and Holmes 1995). Population regulation (*i.e.* bounded fluctuations) and associated mechanisms have received less attention among avian ecologists, which is surprising given that bird populations are among the least variable of all natural populations, suggesting strong regulation (Murdoch 1994).

Rodenhouse et al. (1997) present theory and empirical evidence for a population regulation mechanism they call site dependence. Site dependence has two important premises: variation in site quality (for breeding and/or survival) and preemptive use of sites. These two aspects were first described by Pulliam and Danielson (1991), but Rodenhouse et al. (1997)

focused on the level of individual breeding sites rather than subpopulations in different habitats, and explicitly described consequences for population regulation. Rodenhouse et al. (1997) show through simulation modeling and empirical evidence that if site quality varies continuously (both within and among available habitats) and if individuals use sites preemptively (i.e. always choose best site available and do not share resources with others), site dependence can produce negative feedback required for population regulation. Negative feedback is the result of increased use of sites of progressively lower suitability as population size increases, thus reducing average demographic rates for the population.

This study was designed to assess the habitat distribution of Prothonotary Warblers breeding in a bottomland hardwood forest and to determine if that distribution was consistent with ideal free or ideal preemptive models. Furthermore, using data on habitat selection, site fidelity, and reproductive success, I describe the intersection of individual and population behavior.

Bottomland hardwood forests are a mosaic of community types where habitat configuration is largely determined by small changes in elevation, which dramatically alter hydrology and soils. I first describe density patterns in two primary habitat types and test the influence of age-based behavioral dominance on habitat distribution of territorial males. I ask, based on preliminary data and literature, "Why do Prothonotary Warblers prefer cypress-gum swamp community over mixed hardwood levee community?" and test the hypothesis that average fitness is greater in swamps than in levees. The proximate mechanisms that may result in greater fitness include greater fecundity and/or lower nest mortality. Accordingly, I examined clutch size, fledging rates, and nest survival in each habitat type. Furthermore, if females are limiting, breeding site quality and fitness will depend on the probability of establishing a pair

bond with a breeding female; I compare pairing success between habitats. Return rates to breeding sites and movements between seasons also will reflect habitat quality and provide information on site quality distributions. Based on these results, I also ask, "How does the behavior of individuals influence population dynamics?" My ultimate goal is to describe a mechanism that links population regulation to variation in site quality (both within and between habitats), movement among breeding sites, and habitat-specific demography.

Methods and Study Area

Data Collection and Study Area

Field assistants and I conducted this research in the bottomland hardwood forests of the lower Roanoke River, Martin and Bertie Counties, NC. The entire floodplain of the lower Roanoke River is 612 km^2 and represents the largest remaining area of mature bottomland hardwoods in the Mid-Atlantic region (Rice and Peet 1997). The floodplain is dominated by two forest cover types: "Zone II—River Swamp Forest" and "Zone IV—Forests of Backwaters and Flats" [Christensen, 2000 #397]. These cover types correspond to "Coastal Plain Levee Forest Brownwater Subtype" and "Cypress-Gum Swamp Brownwater Subtype," respectively, of Schafely and Weakly (1990).

These two habitats differ in hydrology, floristics, and structure. The levee forest, usually found on higher, well-drained soils adjacent to the main river channel, is usually only flooded for a short period during the growing season. It is a diverse community with several tree species usually codominant in the canopy: sugarberry (*Celtis laevigata* Wild.), green ash (*Fraxinus pennsylvanica* Marsh.), boxelder (*Acer negundo* L.), American elm (*Ulmus americana* L.), and sweetgum (*Liquidambar styraciflua* L.). The subcanopy often includes pawpaw (*Asimina triloba*

L.), American hornbeam (*Carpinus caroliniana* Walt.), deciduous holly (*Ilex decidua* Walt.) and hawthorns (*Crataegus* L.). Giant cane (*Arundinarea gigantea* Walt.) may occur in dense thickets in the shrub layer, along with pawpaw. These three strata result in substantial vertical and horizontal heterogeneity. The swamp forest has markedly lower plant species diversity. It is found on low, poorly drained soils, away from the main river channel and has semi-permanent or permanent standing water. The canopy is dominated by two tree species: baldcypress (*Taxodium distichum* L.) and water tupelo (*Nyssa aquatica* L.). Occasionally there is a subcanopy of Carolina ash (*Fraxinus carolinana* Mill.*)*, but there is no shrub layer. As a result of lower diversity and a simpler structure, the swamp forest presents substantially less vertical and horizontal heterogeneity than the levee forest.

Prothonotary Warblers are small (about 15 g), mainly insectivorous wood warblers (*Parulidae*). This species is one of only two wood warblers that habitually nests in cavities (Lucy's Warbler [*Vermivora luciae*] of the southwestern U.S. also nests in cavities). Nests are placed not only in natural cavities and crevices, but also in vacant woodpecker and chickadee nest cavities, and nest boxes (Fleming and Petit 1986, Curson *et al.* 1994). Females build the nest, which is a cup of mosses and rootlets lined with finer materials. Eggs are incubated for 12-14 d and nestlings fledge after about 11 d. During the breeding season, the species is widespread in coastal plain lowlands of the Atlantic (from southern New Jersey south to central Florida) and the Gulf of Mexico (from northern Florida west to eastern Texas and central Oklahoma). It is also widespread in the Mississippi and Ohio River valleys north to Wisconsin, Michigan and Ohio (Curson *et al.* 1994, Dunn and Garrett 1997). During the Nearctic winter, Prothonotary Warblers are found from the Yucatan Peninsula south to Panama, Columbia, and Venezuela (American Ornithologists' Union 1983).

To study the abundance, distribution, and demography of Prothonotary Warblers on the lower Roanoke River, I established six study plots (three each in levee and swamp forest). Warbler density was significantly greater in swamp forest (see Results); in order to keep the number of birds studied on each plot roughly equal, swamp plots were 6.25 ha whereas levee plots were 12.5 ha. Plots were at least 500 m from each other and were interspersed along a 50 km stretch of the river. Each plot contained a 25 x 25 m grid of small plastic flags to facilitate censuses and nest monitoring. Plots were monitored from late April, before the birds arrived, until all nesting attempts were complete, usually by early July. In 1995, the first year of the study, only levee plots were monitored; in 1996-1997 both levee and swamp plots were studied. We also collected supplemental nest data from other levee plots identical to the primary study plots as part of ongoing studies of bird populations in 1995. All plots were visited in mid-May 1998 to gather information on return rates.

Using mist nets and playbacks of territorial song, we captured most (>95%) territorial males and marked each bird with a unique combination of colored leg bands. Captured males were placed in one of two age classes, "yearling" or "older male", based on plumage characteristics (Pyle *et al.* 1987). Yearlings were individuals that hatched in the previous breeding season and were in their first potential breeding season; older males were individuals in their second or subsequent potential breeding season.

We delineated all territories on each plot every 10 d using the spot map method (International Bird Census Committee 1970) and more detailed observations of color-marked individuals. Banded males were followed and their positions were recorded on gridded maps of the study plots. Simultaneous singing of adjacent males and antagonistic interactions helped delineate territory boundaries. Also recorded on study plot maps were presence of females,

courtship and nesting behaviors, and presence of fledglings. Pair-bond status was inferred from spot maps and intensive searches of all territories for nests throughout the season. If a territorial male and female were repeatedly observed interacting during the course of the breeding season, it was assumed that they had established a pair bond. Warbler density estimates were adjusted for the fraction of each territory on the plot, and final density estimates were expressed as the number of birds (males and females) per 10 ha (Holmes *et al.* 1986).

Nests were found by intensively searching study plots throughout the season and by following any female encountered on or near the plots. We visited active nests every three or four days and recorded the contents (number of eggs or young), if visible, or noted parental behaviors that indicated nesting stage. If expected hatching date was known, or could be estimated from development of young, nests were checked when nestlings were nine days old to determine fledging success. Day nine was chosen to avoid premature fledging of young as a result of disturbance. If the nest was active and contained fully feathered young on day 9, the nest was considered successful. Nest survival estimates were calculated using the Mayfield method (Mayfield 1961, Mayfield 1975). Mayfield estimates are point estimates of the probability that an active nest will survive one day, and are based on the ratio of number of nest failures to number of days that active nests are exposed to mortality agents. Probability of nest survival throughout incubation and nestling periods combined can be estimated through extrapolation of the daily probability of nest survival. For nests that fail, mortality is assumed to have occurred at the midpoint between the last two nest checks. I compared Mayfield estimates for each habitat using the methods of Hensler and Nichols (1981).

Statistical Methods and Return Rates

Bird density, clutch sizes, and fledging rates between habitats were compared using Wilcoxon rank sum tests. Because clutch size often decreases during the breeding season, I used only early nests and confirmed first nest attempts from monitored territories when testing differences in clutch and brood sizes. Early nests were defined as nests initiated (*i.e.* incubated) on or before 15 May, a cutoff date based on the distribution of initiation dates. Median and mean nest initiation dates were 13 and 16 May, respectively. The cutoff date was in the 12th percentile of nest initiation dates for confirmed first nest attempts. It is thus unlikely that many second nest attempts were initiated before 15 May in this system. Nests that failed before clutch completion were not included. To determine if clutch and/or brood sizes were more variable in one habitat than the other, I used the Moses two-sample dispersion test (Moses 1963, Hollander and Wolfe 1973). The Moses test randomly divides each habitat sample into equal subsamples, calculates sums of squares for each subsample, and then compares the magnitude of the sums of squares values using a Wilcoxon rank sum test.

I tested differences between habitats in the age distribution of males and pairing success using Fisher's exact test for 2×2 contingency tables. Logistic regression models were used to evaluate the influence of habitat and male age on pairing success, success of first nest attempts, and overall success (fledge at least one nest vs. none). Post hoc power analyses for the 2×2 contingency tables were conducted using Gpower software (Erdfelder *et al.* 1996).

Return rate is the product of two probabilities: the probability of survival during the nonbreeding season and the probability of returning to the same nest plot in the following spring. Return rate is thus a function of survivorship and site fidelity. Formal mark-recapture analyses are designed to separate these two life history traits and often provide estimates of survivorship.

The mark-recapture data from this study are insufficient to provide habitat specific estimates of survivorship. Nevertheless, one can examine mark-recapture summaries and return rates for patterns that may reflect overall habitat quality.

First, I examined overall return rate in each habitat. Overall return rate is the ratio of individuals recaptured each year to total marked in *all* previous years. Second, I also examined "year-to-year" return rate because overall return rate may mask important heterogeneity among individual birds. Year-to-year return rate is the ratio of individuals recaptured each year to total marked in the penultimate year only. In a mark-recapture study, each breeding season represents a capture event. Theoretically, all birds are released at the end of each capture event. In every year but the first year of the study, these releases were comprised of two classes of individuals: those "recaptured" (i.e. resighted), having been banded in a previous breeding season (residents), and those captured for the first time (immigrants). I used year-to-year return rate as a measure of breeding site fidelity of immigrants.

Results

Population Structure

Bird density was fairly constant from year to year on both levee and swamp plots (Table 2.1); there were no extreme population fluctuations during the study period. Overall bird density, however, was markedly greater on swamp plots than on levee plots (Wilcoxon rank sum test, $Z = 3.12$, $P = 0.002$, $n = 15$ plot-years). The annual mean number of birds (males and females) per 10 ha was 7.4 (± 3.0 SD, $n = 3$) on levee plots and 23.3 (± 6.7 SD, $n = 2$) on swamp plots. I monitored 126 territories, 62 in levee forest and 64 in swamp forest. Territories tended

to be smaller and more tightly packed in swamp forests than levees. Consequently, there was more unoccupied space in levee forests. Bird density was more variable in levee forest (variance ratio test, $F(5,8) = 5.09$, $P = 0.04$).

Age structure of the population was similar in the two habitats (Table 2.1). There was just as high a proportion of older males (two years or older) on levee plots as on swamp plots (Fisher's exact test, $P = 0.69$, $n = 115$). Power analyses indicated that this test had sufficient power (≥ 0.90) to detect moderate or large effects; if habitat type is associated with age distribution, it is a small effect (i.e. effect size < 0.30). In each habitat type, about two-thirds of the territory holders were older males and the remainder yearlings.

Territorial males in swamp forest were more likely to be paired with a breeding female than males in levee forest (Table 2.1, Fisher's exact test, $P = 0.002$, $n = 114$). In levee forest each year, 29-36% of males did not have a mate, whereas only 7-10% were without mates in swamps (Table 2.1). Older males were more likely to have a mate than yearlings in both habitats (Table 2.2, Fig. 2.1).

Reproductive Success

Breeding pairs made 110 nest attempts; attempts per pair ranged from zero to three. Average clutch size was greater in swamps (5.0 ± 1.0 SD) than levees (4.0 ± 1.2 SD) (Wilcoxon rank sum test, $Z = -3.04$, $P = 0.002$, $n = 47$, Fig. 2.2). Birds nesting in swamps also fledged more young per nest than those nesting in levees ($Z = -1.99$, $P = 0.047$, $n = 27$, Fig. 2.2). Mean number of fledglings per nest was 4.8 (± 1.1 SD) and 3.7 (± 1.4 SD) for swamps and levees, respectively. Mayfield nest success estimates, however, did not differ between the two habitat types ($Z = 0.82$, $P = 0.21$, Table 2.3). The daily probability of nest survival was 0.963 and 0.955

for levee and swamp forests, respectively. Levee clutches tended to be more variable than swamp clutches (W = 58, P = 0.12, n = [6, 9]), and levee brood sizes were more variable than swamp brood sizes (W = 25, P = 0.03, n = [4,4]). Maximum clutch size observed in levees was five eggs; maximum clutch size in swamps was six. Habitat quality, as reflected in reproductive success, was thus more variable in levees than in swamps (see also Fig. 2.2).

In swamps, older males and yearlings had equal success with the initial nest attempt of the season. In levees, however, older male success with first nests was greater, and yearling male success was lower, than in swamps (Fig. 2.3). Male age and the interaction of male age and habitat thus influenced the probability of success on first nest attempt, although these effects were significant only at the 0.08 level (Table 2.2). Older males were more successful overall (one successful nest vs. none) than yearling males, regardless of habitat (P < 0.05, Table 2.2). The overall fit of data to these two logistic regression models was marginal in each case (0.09 < P < 0.12), indicating that much variation in success rates remains unexplained. Nevertheless, these models suggest that older males are more successful than yearlings and may occupy better breeding sites in each habitat.

Return rates and Site Fidelity

Each year of the study, total number of birds "captured and released" ranged from 16-35 in levee forest and from 27-32 in swamp forest (including resighting of birds previously marked; Table 2.4). No males moved between study plots. In only two cases did a bird return to a study plot after spending a breeding season outside the plot; this occurred once in each habitat type (Table 2.4). In each case the territorial male was banded on the study plot edge and likely shifted his territory away from the plot boundary and was undetected. Overall return rate (ratio of

individuals recaptured each year to total marked in all previous years) was not significantly different in levees and swamps (28% levee vs. 39% swamp [Table 2.4], power = 0.93). There was, however, significant heterogeneity among individuals in each habitat. Year-to-year return rate (ratio of individuals recaptured each year to total marked in previous year only) was higher in swamps than in levees (21% levee vs. 39% swamp [Table 2.4]).

Immigrants were significantly less likely to return to levee territories than residents (Fisher's exact test, P = 0.02, n = 35); return rates for the two classes of individuals did not differ in swamps (Fisher's exact test, P = 0.70, n = 32). Statistical power was sufficient (> 0.80) for these tests to detect large effects, but power was low for moderate and small effect sizes. Nevertheless, residency status affected return rates in levees but not in swamps. Age distribution of immigrants was similar between habitats (levee: [11/19] 58% yearling; swamp: [10/19] 53% yearling).

Discussion

Habitat selection behavior and fitness consequences for Prothonotary Warblers breeding on the lower Raonoke River are consistent with the ideal preemptive distribution, rather than ideal free. Prothonotary Warblers occur at higher densities, and more importantly, produce more young on average in cypress-gum swamps than in coastal plain levees, a critical difference between ideal free and ideal preemptive model predictions (Fretwell and Lucas 1970, Pulliam and Danielson 1991). Density alone may be a misleading indicator of habitat quality (Van Horne 1983). When used in combination with fecundity data in this study, however, results indicate that, on average, swamps are a more suitable habitat. Increased reproductive success in swamp habitats was the result of greater average clutch and brood sizes as opposed to increased nest

survival; nest survival rates and predation pressure appear to be equal between habitats. Indirect evidence suggests that food resources are greater in swamps than in levees (see Chapter 3), and variation in food resources may have allowed birds nesting in swamps to produce bigger clutches. Thus, Prothonotary Warblers prefer cypress-gum swamps in this system as a result of habitat-specific demography and concomitant fitness benefits for most birds breeding in swamps.

Ideal preemptive distributions appear to be common among breeding birds that defend all purpose feeding and nesting territories because individuals generally gain exclusive use of resources (preemption). Many earlier studies of breeding birds have found evidence consistent with ideal-despotic/preemptive models (Krebs 1971, Andren 1990, Moller 1991, Dhondt et al. 1992, Tregenza 1995, Petit and Petit 1996). Andren (1990) studied European Jays in 12 different habitat types and found that individuals preferred dense forests dominated by Norway Spruce with trees > 10 yr old. Territories in spruce habitat experienced lower rates of nest loss, consistent with ideal despotic/preemptive distribution. Results indicated that predation rates were lower in preferred areas, but food resources also may have influenced breeding success (Andren 1990).

Moller's (1991) comparative study found support for the ideal despotic/preemptive model among seven species breeding in woodlots in an agricultural landscape. For species that rely on local food resources and/or suffer high nest predation rates, age-related behavioral dominance resulted in fewer young birds in areas of high reproductive success (large habitat patches) [Moller, 1991 #22]. For species that rely on food resources outside their territory (e.g. colonial passerines), age distribution did not change with habitat area, and Moller (1991) concluded that "ideal free distribution for unequal competitors" was supported (Sutherland and

Parker 1985). Moller (1991) thus found nest sites (i.e. shelter from predators) and food resources as important influences on habitat distribution.

Petit and Petit (1996) studied the habitat selection of Prothonotary Warblers nesting in artificial and natural nest cavities in bottomland habitats along the Tennessee River in Tennessee. They established replicate study plots at the river edge, each containing a grid of nest boxes. Warblers preferred the wetter territories closer to the river and these areas were dominated by older males (Petit and Petit 1996). These preferred areas were settled earlier and produced more young in the absence of predation losses (Petit and Petit 1996). Petit and Petit (1996) conclude that Prothonotary Warblers breeding in Tennessee bottomlands are distributed among habitats according to the ideal dominance (i.e. preemptive) model of Fretwell and Lucas (1970) and that dominance is presumably age-related because older males prevailed in wetter areas.

Holmes et al. (1996) described the habitat-specific demography of Black-throated Blue Warblers and discussed implications for population dynamics. Their study included two kinds of study plots that differed in shrub density. Black-throated Blue Warbler densities were higher, and individuals fledged more young per season, in areas of high shrub density than in areas of low shrub density. Increased reproductive success was mainly due to frequency of double brooding on high shrub density plots, rather than differences in clutch size, unlike in this study. Holmes et al. (1996) also found a strong correlation between age and habitat type: older individuals were more abundant on high shrub density plots.

Although cypress-gum swamp appears to be a more suitable habitat and preemptive use of sites seems likely, age distributions observed in this study are not consistent with previous studies that found ideal preemptive distributions. Equal proportions of adult males were found in cypress-gum swamps and coastal plain levee forests, and yearlings were not prevented from

settling in swamps. One possible explanation for this pattern is that age-related dominance does not operate in this system. This seems unlikely given the results of numerous studies supporting the existence of age-based behavioral dominance in warblers and other passerines (Lanyon and Thompson 1986, Sherry and Holmes 1989, Andren 1990, Holmes et al. 1996, Petit and Petit 1996). Adult male passerines often hold territories in preferred habitats and prevent subordinant young males from settling, or force them to settle in less suitable habitats.   Indeed, Petit and Petit (1996) found evidence of behavioral dominance among male Prothonotary Warblers in Tennessee.

An alternative explanation is that male age distribution between habitats is the result of different site quality distributions in each habitat and breeding site fidelity of older males. Site quality distributions can be modeled as an exponential function (Pulliam and Danielson 1991). A high quality habitat, rich in resources, and a low quality, poor habitat would have two different site quality distributions (Fig. 2.4). Despite the differences in mean site quality between rich and poor habitats, the poor habitat has some good breeding sites, along with many low quality sites. The rich habitat is composed of mostly good breeding sites, with few low quality sites. Adult males in levee forest probably occupy the good breeding sites found there. Pairing success data support this interpretation. Pairing success was influenced by both habitat and male age; older males were paired with a breeding female more often than yearlings in levees. Success of first nest attempts also indicates that older males occupy higher quality sites than yearlings in levees. Older males on levees were the most successful of all age-habitat classes in first nest attempts (Fig. 2.3). Once a male has a good territory on the levee, it appears that he is unlikely to move from that site. Return rates indicate strong site fidelity by older males on levees, unlike in swamps. Returning birds occupied the same territories each year and were not observed making

significant shifts within plots. Holmes and Sherry (1992) found a similar pattern of low site fidelity to first potential breeding site, followed by high site fidelity unrelated to breeding success in American Redstarts. Other studies have found strong site fidelity by breeding males (Lanyon and Thompson 1986, Beletsky and Orians 1987). Thus, site quality distributions and site fidelity may account for the dominance of older males in both levees and swamps.

This does not mean that all yearlings are relegated to low quality sites. In swamps, where site quality distributions suggest that there are mostly good sites, yearlings probably occupy at least moderate territories. There are more individuals shifting territories in swamps, however. Return rates of residents and immigrants in swamps indicate different patterns of site fidelity relative to levee, a difference that may be explained by intrusion pressure. If site fidelity is a function of intrusion pressure, it is probably more difficult to return to the exact same swamp territory year after year, given the relatively high bird density there. In addition, the cost to shifting territories, if any, may be lower in swamps given a high proportion of high quality sites. Holmes et al. (1996) showed that young male Black-throated Blue Warblers had significantly lower local survival on low quality sites and suggested that young males were more likely to move between seasons in an attempt to improve their breeding site quality. Results of this study also indicate significant movement among territories by males, possibly in an attempt to improve site quality, but immigrants were a mix of yearlings and older birds, rather than predominantly yearlings.

Rodenhouse et al. (1997) suggest that site dependence is a mechanism of population regulation operating at the level of individual breeding sites. Site dependence theory is a synthesis and extension of several theoretical and empirical studies, including ideal-despotic and preemptive models (Fretwell and Lucas 1970, Fretwell 1972, Pulliam 1987, Pulliam and

Danielson 1991), source-sink dynamics (Pulliam 1988), and effects of habitat-heterogeneity

(Dhondt et al. 1992, Ferrer and Donazar 1996). As noted above, results of this study are

consistent with the ideal preemptive distribution. Ideal preemptive habitat use has strong ties to

the source-sink model. Source and sink habitats differ in their site quality distributions (Fig. 2.4;

(Pulliam and Danielson 1991). As site quality distributions for two habitats diverge, one habitat

eventually becomes a source and the other a sink. It is not clear if the site quality distributions

for swamps and levees are disparate enough to act as source and sink. Assuming adult and

juvenile survival rates typical of Nearctic-Neotropical migrants, Prothonotary Warblers would

need to fledge about 3-4 young per pair to maintain a steady state population (Holmes et al.

1992, Sherry and Holmes 1995, Holmes et al. 1996). In this study, offspring production in each

habitat appears adequate to maintain a steady state and source-sink dynamics appear unlikely.

Source-sink dynamics and ideal preemptive distribution emphasize subpopulations living

in different habitats. Habitat-specific demography (as demonstrated for Prothonotary Warblers

in the lower Roanoke River) is an important factor in recognizing these phenomena. The best

model to describe the intersection of individual and population behavior, however, is site

dependence because it operates at the level of individual breeding sites.

Site dependent population regulation has two major features: 1) variation among sites for

reproduction and/or survival as a result of environmental heterogeneity, and 2) preemptive use of

sites, with movement of individuals to higher quality sites as they become available (Rodenhouse

et al. 1997). Evidence exists for both features in this study. Variation in site quality is reflected

in overall variation in clutch and brood sizes (Fig. 2.2); this variation is greater in levees than in

swamps. Age and experience of the breeding pair explain some of this variation, but small

sample sizes did not permit direct assessment of these effects. Age of the breeding female in

particular may influence reproductive success, and it may be that females breeding in swamps are older than those breeding in levees. No data on female age were collected so it is not possible to evaluate this possibility. Pairing success also indicates significant site quality variation. Some territories, especially on levees, are rejected by breeding females (whether females are limited or not), and quality of these sites is presumably well below average. The second premise of site dependent regulation, preemptive use of sites, follows successful territorial behavior. Evidence in this study for preemption includes habitat-specific demography and associated density patterns, and evidence for older males on high quality levee territories. Thus, breeding males are using the best site available to them and preempting resource use by others. Finally, movement to higher quality sites is strongly indicated by site fidelity patterns on levees: immigrants (who were likely on the lowest quality territories) did not return to those territories as often as residents and were probably attempting to improve the quality of their site.

This study represents a partial test of site dependent regulation and as such contributes knowledge about the regulatory role of this mechanism (Rodenhouse et al. 1997). The main features of this mechanism, variation in site quality and preemptive site use, are present for Prothonotary Warblers breeding in the bottomlands of the lower Roanoke River. Future research should include experimental manipulations that will provide a direct test of the potential for site dependence to regulate bird populations. For cavity nesting species, it may be possible to manipulate nest site resources on random territories and monitor occupancy rates, characteristics of territory owners, and reproductive success. Site dependence predicts that poorly provisioned sites will only be occupied as population size increases and that average demographic rates will be lowered as a result.

Acknowledgements

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Table 2.1. Density, age structure, and mating patterns of Prothonotary Warblers in coastal plain levee and cypress-gum swamp forest habitats, 1995-1997.

	1995	1996	1997	1995-1997
Bird density (# per 10 ha, mean ± SD)[a]				
Levee	8.1 ± 3.9	7.1 ± 1.4	7.1 ± 4.0	7.4 ± 3.0
Swamp	-	23.5 ± 3.2	23.1 ± 10.0	23.3 ± 6.7
Male Age Composition: % older males (n)				
Levee	70% (24)	73% (19)	63% (16)	69% (59)
Swamp	-	63% (27)	66% (29)	64% (56)
Mating Patterns: % males unmated (n)				

Levee	36% (22)	29% (17)	35% (17)	34% (56)
Swamp	-	10% (30)	7% (29)	8% (59)

[a] n = 3 plots per forest type; includes males and females

Table 2.2. Logistic regression models for probability of pairing success, success in first nest attempts only, and overall success each year (fledge at least one nest vs. none) for territorial males. Independent variables include habitat (levee forest or cypress-gum swamp) and male age (yearling or older male). The likelihood ratio chi-square test has one degree of freedom for each parameter and 3 df for the model including all parameters.

Response	Parameter	Parameter Estimate	SE	χ^2	P
Pairing success (n = 104)	Intercept	-0.357	0.493	0.524	0.469
	Habitat	1.897	0.805	5.557	0.018
	Age	1.455	0.625	5.417	0.019
	Habitat × Age	0.501	1.35	0.137	0.711
	Model	…	…	21.510	<0.001
First nest attempt (n = 64)	Intercept	-1.099	1.155	0.905	0.341
	Habitat	1.253	1.282	0.955	0.328

	Age	2.262	1.263	3.206	0.073
	Habitat × Age	-2.490	1.433	3.019	0.082
	Model	…	…	5.970	0.113
Overall success (n = 68)	Intercept	-0.693	0.866	0.641	0.424
	Habitat	0.693	1.018	0.464	0.496
	Age	1.966	0.966	4.144	0.042
	Habitat × Age	-1.436	1.174	1.496	0.221
	Model	…	…	6.462	0.091

Table 2.3. Mayfield nest success estimates for Prothonotary Warblers breeding in coastal plain levee and cypress-gum swamp forest habitats, 1995-1997. Nest exposure days is the cumulative total number of days that active nests were monitored.

Forest type	No. nests	Nest exposure days	Daily probability of nest survival	Nest survival variance	95% confidence interval	Mayfield nest success estimate[a]	Percent successful[b]
Levee	74	892	0.9630	0.00004	(.9506, .9754)	0.4046	55%
Swamp	61	755	0.9549	0.00006	(.9401, .9697)	0.3307	44%

[a] (daily prob. of nest survival)^k ; k = # days in nest cycle = 24

[b] percent successful = proportion of nests fledging at least one nestling

Table 2.4. Recapture data (A) and return rates (B) for Prothonotary Warblers in two
breeding habitats, levee forest and cypress-gum swamp forest. Each row in (A) is a
combination of newly banded birds and previously banded birds released in the same
year.

A. Mark-recapture data

Released		Year Next Captured			
Year	Number	1996	1997	1998	Never Recaptured
Levee forest					
1995	35	9	1	0	25
1996	23		8	0	15
1997	16			4	12
Swamp forest					
1995	-	-	-	-	-
1996	27		13	1	13
1997	32			10	22

B. Return rates

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Return Rate	Levee forest		Swamp forest		P^a
Recaptured (year i + 1)[b]	$\underline{21} =$	0.284	$\underline{23} =$	0.390	0.26
Marked (any year)	74		59		
Recaptured (any year)[c]	$\underline{22} =$	0.297	$\underline{24} =$	0.407	
Marked (any year)	74		59		
Recaptured (year i + 1)[b]	$\underline{12} =$	0.211	$\underline{18} =$	0.391	0.05
Marked (year i)	57		46		
Recaptured (any year)[c]	$\underline{13} =$	0.228	$\underline{19} =$	0.413	
Marked (year i)	57		46		

[a] Fisher's Exact Test

[b] Estimates the product of survival and recapture probabilities, neglecting variations in recapture probability over time.

[c] Does not estimate the product of survival and recapture probabilities because individuals have been exposed to several recapture occasions.

Figure 2.1. Pairing success of territorial males in two habitats and two age classes. Yearling males are in their first potential breeding season and older males are in their second or subsequent breeding season. Sample sizes are above each bar.
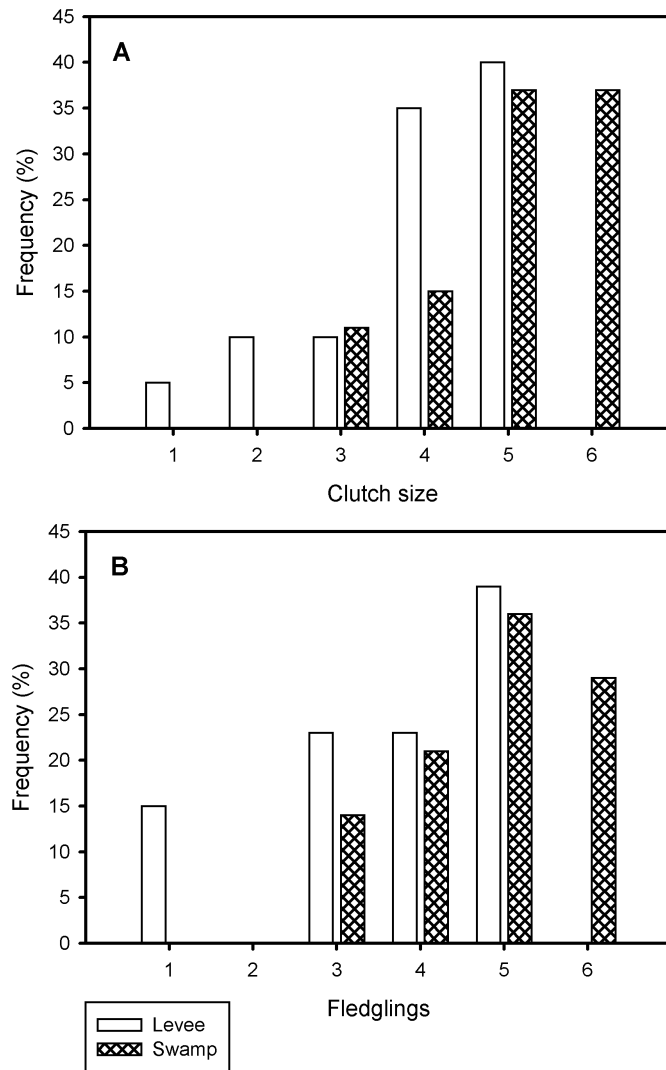
Figure 2.2. Frequency distribution of clutch size (A) and fledglings per successful nest (B) for

Prothonotary Warblers in levee forest and cypress-gum swamp forest. Sample sizes are 47

(levee, n = 20; swamp, n = 27) for clutch size data and 27 (levee, n = 13; swamp, n = 14) for

fledgling data.

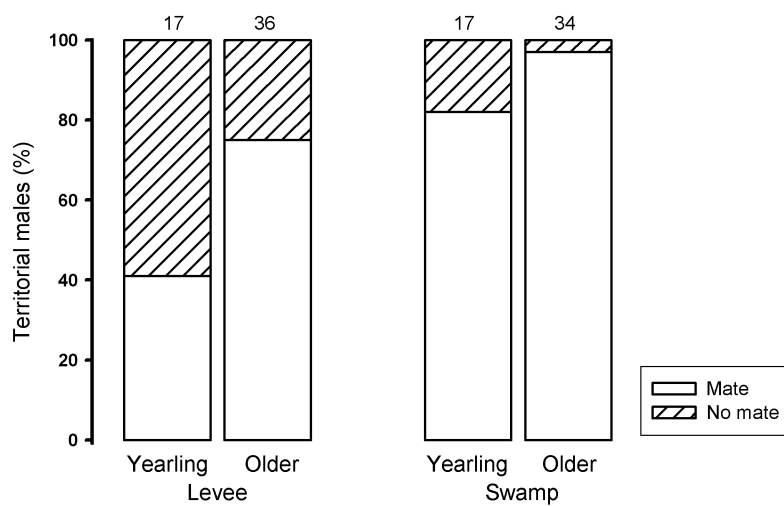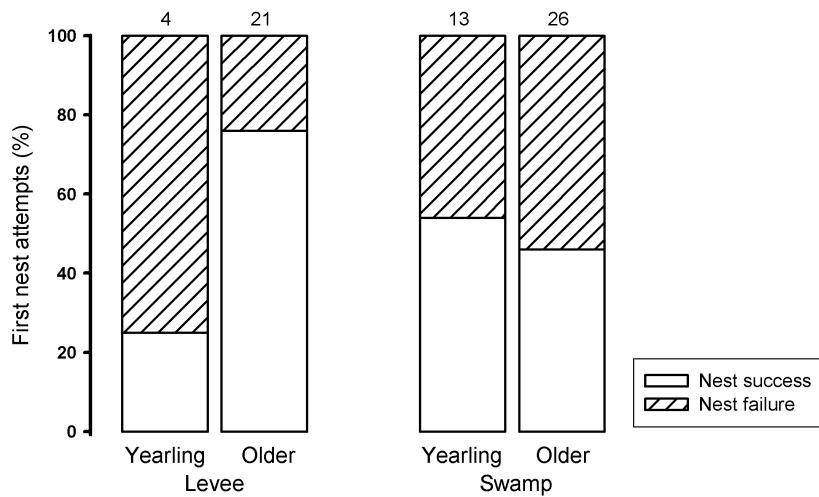Figure 2.3. Nest success on first nest attempts for territorial males in two habitats and two age

classes. Yearling males are in their first potential breeding season and older males are in their

second or subsequent breeding season. Sample sizes are above each bar.
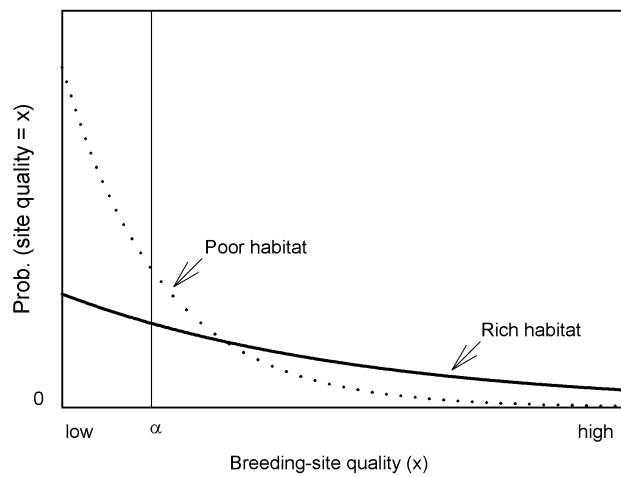
Figure 2.4. Site quality distributions for two habitats with different mean reproductive success, based on Pulliam and Danielson's (1991) exponential model of site quality. Rich habitats have more resources and a greater proportion of high quality sites, and hence higher mean reproductive success. α represents theoretical minimum acceptable site quality, below which sites are not used.

CHAPTER 3. HABITAT-SPECIFIC FORAGING OF PROTHONOTARY WARBLERS: DEDUCING HABITAT QUALITY

Abstract

Foraging behavior often reflects food availability in a variety of ways. For example, in habitats where food availability is high, predators should move more slowly and attack prey more often than in habitats where food availability is low. I studied the foraging behavior of breeding Prothonotary Warblers in two habitat types to assess relative food availability and implications for habitat quality. In the floodplain of the lower Roanoke River in North Carolina, Prothonotary Warblers breed in two distinct habitats: cypress-gum swamp forest and coastal plain levee forest. These two habitats differ in hydrology, forest structure, and tree species composition. Swamp forest appears to be more suitable breeding habitat because warbler density is three times higher and breeders have greater reproductive success in swamps than in levees. I quantified foraging behavior with focal animal sampling and continuous recording during foraging bouts. I measured two aspects of foraging behavior: 1) prey attacks per minute, using four attack types (glean, sally, hover, strike), and 2) number of movements per minute (foraging speed), using three types of movement (hop, short flight [≤ 1 m], long flight [>1 m]). Male warblers made significantly more prey attacks per minute in swamp forest than in levee forest; the same trend was evident in females. Foraging speed, however, was not different between habitats for males or females. Results indicate that foraging effort is similar in swamps and levees, but that warblers encounter more prey in swamps. Greater food availability may be related to greater reproductive success of warblers nesting in cypress-gum swamps than in coastal plain levee forest.

Introduction

Breeding passerines often are distributed among habitats in a nonrandom pattern, with certain habitat types consistently supporting greatest densities. Abundance within a habitat reflects interactions among species (Rosenzweig 1991, Werner 1992) and available resources, among which food may be paramount (Brown 1969, Fretwell and Lucas 1970, Pulliam 1988, Dias 1996, Gordon 1997). Food supply is important because males and females experience time and energy constraints during the breeding season (Martin 1987, 1992). Spatial variation in prey abundance thus is likely to influence not only bird abundance and distribution, but also reproductive success. Assessment of differences in food supply among habitats may reveal insights about habitat quality.

Individuals respond to resource abundance and predation risk when making habitat choices (Werner 1992). The distribution of food among habitats thus affects the distribution of individuals in space, patterns that are responsible for source-sink and metapopulation dynamics. Food resources and foraging behavior help explain patterns of distribution in nature because survival and reproduction ultimately depend on an individual's ability to acquire and use energy from food resources (Hutto 1990b). I measured foraging behavior of prothonotary warblers (*Protonotaria citrea*) in two different habitats during the breeding season and evaluated implications for reproductive success and habitat quality.

Prothonotary warblers are common in most types of bottomland hardwood forest on the lower Roanoke River in North Carolina (Sallabanks *et al.* 2000). These habitat types can be broadly classified using two categories, coastal plain levee forest (levee) and cypress-gum swamp forest (swamp), which differ in hydrology, soils, vegetation structure, and plant species composition (Schafale and Weakley 1990, Rice and Peet 1997). Although *P. citrea* is a

dominant member of avian assemblages in both levees and swamps, warbler density is

significantly greater in swamps (e.g., swamps: 23.3 ± 6.7 SD males and females per 10 ha; levee:

7.4 ± 3.0 SD; see Chapter 2). Furthermore, average clutch size (5.0 ± 1.0 SD) and fledglings per

successful nest (4.8 ± 1.1 SD) are significantly greater in swamps than levees (4.0 ± 1.2 SD and

3.7 ± 1.4 SD for clutch size and fledglings, respectively; see Chapter 2). Nest predation rates,

however, are similar between habitats; daily probability of nest survival was 0.96 in swamps and

levee (see Chapter 2). As part of ongoing studies of population ecology of prothonotary warblers

in the Roanoke River basin, I evaluated foraging behavior and investigated the possibility that

greater bird density and greater reproductive success in swamps was at least in part based on

food resources.

I measured foraging behavior rather than sampling prey because studies of foraging

behavior may reveal as much about prey abundance and distribution as attempts to sample prey

populations (Hutto 1990a). Several aspects of foraging behavior have predictable relationships

with prey abundance, and provide information on food availability (Gibb 1954, Thiollay 1988,

Hutto 1990a). These behaviors can therefore be appropriate surrogates or complements to

estimates of mean prey levels (Hutto 1990a, Lovette and Holmes 1995). The functional response

of predators to variation in prey density, however, varies among taxa (Holling 1965, Abrams

1982, 1990, Schluter 1984, Holmes and Schultz 1988).

Prey availability has strong implications for two aspects of foraging behavior: attack rate

and search speed. Recent experimental and observation studies have documented a positive

correlation between attack rate of avian predators and prey density. Delestrade (1999) provided

supplemental food to alpine choughs (*Pyrrhocorax graculus*) and found that attack rate,

measured in pecks per minute, increased with total quantity of food. Similarly, Shepherd and

Boates (1999) found peck rate, capture rate, and percent successful pecks of foraging

semipalmated sandpipers (*Calidris pusilla*) were correlated with prey density in coastal mudflats.

Attack rates increase with prey density in a wide variety of bird families: Charadriidae (Baker

and Baker 1973, Loegering and Fraser 1995, Elias *et al.* 2000), Tyrannidae (Hutto 1981,

Blancher and Robertson 1987), Turdidae (Smith 1974, Greenwood and Harvey 1978,

Paszkowski 1982), Motacillidae (Davies and Houston 1981, Brodmann *et al.* 1997a), Parulidae

(Robinson and Holmes 1984), and Fringillidae (Schluter 1984). Search speed has received less

attention in the literature. Studies of shorebirds and ground-foraging passerines, however,

suggest that searchers move more slowly after capturing prey and when in areas with high prey

density (Baker 1974, Smith 1974, Zach and Falls 1976, Zach and Falls 1979, Pienkowski 1983).

Attack rates and search speeds are thus indicators of food supply. In addition, nestling feeding

rate and time-activity budgets also are correlated with prey levels (Davies and Lundberg 1985,

Blancher and Robertson 1987).

Most passerines are insectivorous during reproduction and lepidopteran larvae dominate

the diets of foliage-gleaning species. Sampling of insect prey populations within and between

habitats is complicated by spatial and temporal variation in prey abundance. Prey items are often

aggregated and prey populations fluctuate during the breeding season and between years (Majer

et al. 1990, Smith and Rotenberry 1990). When comparing prey samples from different habitats,

variances of mean estimates often are so great that statistical significance is improbable even

when biological significance seems likely. Adequate statistical power requires large samples,

often collected at considerable expense of time and money. Avian prey sampling is further

complicated by perceptual differences between investigator and subject; it is difficult to

determine which prey are truly available to foragers, let alone what foragers prefer (Hutto 1990a,

Poulin and Lefebvre 1997, Blackwell *et al.* 1998). Hutto (1990a) lists two additional pitfalls of

avian prey sampling: identification of the appropriate scale of sampling (e.g. leaf, branch, tree,

territory, etc.) and measurement of prey renewal rates in addition to standing crop. Thus,

obtaining precise and accurate estimates of abundance of relevant prey is labor-intensive and

formidable (Robinson 1998).

To relate foraging behavior to habitat quality, I relied on the empirical studies outlined

above and optimal foraging theory. Optimal foraging theory primarily is concerned with diet

(*i.e.* prey selection) and exploitation of habitat patches (Pyke 1984, Stephens and Krebs 1986),

but also may be used to generate predictions about attack rate and search speed. The common

currency upon which different theories are based is long-term net average energy intake, or

energy per unit time [e_i / t_i (Schoener 1987)]. An important component of all mathematical

descriptions of optimal foraging is mean search time per prey item, which is a function of overall

prey abundance and search velocity (Schoener 1987). Mean search time per prey item decreases

as overall prey abundance or search velocity increases. Foraging animals thus increase net

energy gains by foraging in an area of high food abundance and/or by increasing search velocity.

Predators often decrease search velocity after capturing prey, and search in a restricted area

(Smith 1974, Zach and Falls 1976, Zach and Falls 1979, Pienkowski 1983). Using this simple

application of optimal foraging theory, I predicted that prothonotary warblers should attack prey

more often when foraging in swamps than in levees, and/or that they should search faster when

foraging in levees than in swamps.

Unfortunately, there are no quantitative studies of foraging behaviors that indicate prey

availability within a single season and among habitats (i.e. with implications for relative habitat

quality. Prior research has focused primarily on interspecific comparisons of foraging behavior,

often in a single habitat (Wiedenfeld 1992, Robinson and Holmes 1982, Robinson and Holmes 1984). In a notable exception, Lovette and Holmes (1995) assessed relative food availability for American redstarts (*Setophaga ruticilla*) during breeding and nonbreeding seasons. They measured attack rates, search speed, and other aspects of foraging ecology and convincingly argued that food resources are more abundant for this species on the breeding grounds than in wintering areas. Similar to Lovette and Holmes (1995), my goal was to use foraging behavior to deduce habitat quality, but I focused on two habitats within one phase of the annual cycle rather than a comparison between breeding and nonbreeding seasons.

Methods and Study Area

Field Methods and Study Area

This study was conducted in the swamps and levees of the lower Roanoke River, Martin and Bertie Counties, North Carolina. Swamps have lower tree species diversity, lower stem density of small trees (2.5-8.0 cm dbh), greater stem density of large trees (> 8 cm dbh), and are flooded for a longer duration each year than levees. Observations for this study were made on three study plots in each habitat type. Individual study plots, which were 12.5 ha in levee forest and 6.25 ha in swamp forest, were marked with a 25 x 25 m grid. On each plot, most males (> 90%) were individually marked with colored leg bands, and all territories were delineated using a detailed spot map method. Foraging observations were collected from banded males and unbanded females associated with a particular territory. Based on information from territory monitoring, each foraging observation was classified using four stages of the nest cycle: 1) incubation, 2) feeding nestlings, 3) recently fledged young, and 4) no active nest or young.

Included in the last category are individuals whose nest attempt failed and those that did not attempt a nest.

Field assistants and I made behavioral observations between 20 May and 7 July 1997. I defined the following types of foraging attacks (from Remsen and Robinson 1990):

Glean: from a stationary or hopping position and directed at stationary prey

Sally-hover: from a hovering position and directed at stationary prey

Sally-strike: flying from a perch to attack flying prey

Sally-pounce: from a flying position and directed at stationary prey

I also defined the following foraging movements (after Robinson and Holmes 1982, 1984, Lovette and Holmes 1995):

Hop: powered by legs, no wing movement

Short flight: powered by wings, distance moved ≤ 1 m

Long flight: powered by wings, distance moved > 1 m

Note that "foraging movement" here refers to a type of locomotion and not a foraging "maneuver" (Remsen and Robinson 1990). In addition to the foraging events (attacks and movements) above, we also used several mutually exclusive behavioral states (Altmann 1974):

Search-and-attack: apparently searching foliage and/or the air space nearby, e.g.
    scanning foliage while hopping; the primary foraging state

Handling prey: carrying and manipulating a prey item in the bill; individuals

occasionally held large prey items and repeatedly smashed them on a

branch before attempting to swallow them.

Preening: plumage maintenance

Vigilant: alert; motionless with head up

Singing: males apparently not foraging but perched and singing repeatedly; males

occasionally sang during foraging bouts but it was not their primary

activity

Other: includes aggression, courtship, prospecting for nest sites, and other

activities that were relatively rare

My study design used focal animal sampling and two recording rules during each observation: continuous recording and instantaneous sampling (Martin and Bateson 1986). An observation began once the focal animal was located. Observations continued for as long as the focal individual remained in view (mean duration 122.3 s ± 92 SD). Each observation contained foraging bouts (*i.e.* search-and-attack) and non-foraging bouts (*i.e.* all other behavioral states above). Time devoted to handling prey items was removed from foraging bouts because my main goal was to measure prey attack rates and searching speed. Including handling time in foraging bouts would bias estimates of these rates because an individual presumably cannot search for and attack prey while handling a prey item (Stephens and Krebs 1986). We used continuous recording only during foraging bouts, when observers noted each attack (attempt to capture prey) and each movement (locomotion). Foraging bouts ended whenever the focal individual appeared to stop "search-and-attack" and begin another behavioral state (*e.g.*

preening). In addition to continuous recording during foraging bouts, we used instantaneous

sampling to record behavioral states every 10 s from start to finish of each observation. A

stopwatch with a countdown timer was used to signal the observer at every 10 s sample point. If

a focal animal disappeared from view, the observer had two options. If it appeared that the

animal could be relocated quickly, the observer denoted a "time-out" period to record the amount

of time that the individual was not visible; this time was later subtracted from the observation. If

it appeared that the focal animal would not be quickly relocated, the observer ended the

observation.

We attempted to randomize the order of sampling from all territories, but we also

sampled individuals opportunistically as they were encountered in the field. If a particular

individual was sampled more than once in one day (*e.g.* after having disappeared from view),

observations were summed to give one observation per day.

Observations were recorded in the field using hand-held micro-cassette recorders and

tapes were later transcribed to data sheets. During transcription, 1) all attacks and movements

were tallied, 2) elapsed time of all foraging bouts within each observation was summed using a

cumulative stopwatch, and 3) instantaneous 10 s sample points were tallied. For each

observation, the total number of attacks or moves was divided by the foraging time in seconds to

determine attack rate and search speed, respectively. I used instantaneous sample points to

construct an activity time budget and estimate the amount of time devoted to foraging (*i.e.* the

proportion of all instantaneous sample points that were foraging). Foraging effort was defined as

the proportion of the time budget devoted to foraging. All time-out sample points were removed

from the observation before time budget proportions were calculated.

Statistical analyses

Attack rate, search speed, and foraging effort were analyzed using a robust general linear model (McKean and Vidmar 1994). This rank-based method, which is robust to outliers, was chosen over least-squares methods because the data were severely unbalanced with respect to stage of the nesting cycle. Most observations were from one of two stages, feeding fledglings or no active nest; relatively few observations were from incubation and nestling stages. Severe imbalance in realized design may increase the probability of a type II error for least-squares methods (Shaw and Mitchell-Olds 1993). I used the Kruskal-Wallis test and a multiple comparison of mean ranks to test differences in male search speed among stages of the nest cycle. Proportional response variables were arcsine transformed using the method of Freeman and Tukey (1950, as cited in Zar 1984). Log-linear categorical models were used to describe the association between the types of attacks or movements and sex, habitat, and stage of nesting cycle.   Data were manipulated in two ways, for categorical models only, to eliminate zero cells and raise expected values. First, two nest stages with small samples (incubation and nestling) were not included in categorical models. All four stages—incubation, nestling, recently fledged young, no active nest—were included in general linear models. Second, sally-attacks (sally-hover, sally-strike, and sally-pounce) were pooled, resulting in two types of attacks for categorical models: glean and aerial.

Results

Field assistants and I collected 66 observations of 38 different males (200 min) and 32 observations of 21 different females (68 min). Observations were concentrated in the morning hours between 0830 and 1130.

Attack rates for males and females were greater in swamps than in levees. Both sexes attempted to capture prey items about 2 times per min in levee and 3 times per min in swamps (Fig. 3.1). The evidence of a statistically significant difference between habitats was stronger for males than for females, but sample size of females was smaller (Table 3.1). The entire distribution of attack rates for males and females in swamps was greater than in levees, as predicted (Fig. 3.1). Attack rates appeared equal across stages of the nesting cycle for both males and females, however (Table 3.1). Search speeds of males and females were similar in levees and swamps. Both sexes moved about 15 times per minute in each habitat (Fig. 3.1; Table 3.1). The distribution of search speeds was similar for both sexes in both habitats (Fig. 3.1). Search speed of females did not differ among stages of the nest cycle, whereas speed of males varied among nest stages ($P = 0.06$; Table 3.1). Males moved faster when feeding fledglings than when without an active nest or young; the other nest stages (incubation and nestling) were not distinguished due to small samples.

Males and females used about 82% gleans and 18% aerial attacks; these proportions did not appear to vary with sex (males: 80.1% glean; female 84.3% glean; $P = 0.10$; Table 3.2). The proportion of gleans varied with habitat and stage of nest cycle, however. This effect resulted from a divergent foraging strategy in a single habitat-nest stage category. Swamp birds that were not feeding fledglings used more gleans (about 90%) than swamp birds with fledglings or levee birds in either stage (about 80%). Without fledglings, swamp birds thus reduced use of aerial attacks (Fig. 3.2). Males and females both used about 70% hops, 20% short flights, and 10% long flights and these proportions did not appear to differ between habitats or stages of the nest cycle (Table 3.2).

Females devoted more time to foraging in levees than in swamps (Fig. 3.3; Table 3.3). Females on levees spent 98% of their total time budget in foraging, whereas females on swamps foraged only 68% of the time. The time budget of females did not appear to change with stage of the nesting cycle (Table 3.3). In contrast to females, and predictions based on literature, males spent more time foraging in swamps than in levees. Males also spent more time foraging when they attended recently fledged young than at other stages of the nest cycle (incubation, nestling, not active nest).

Discussion

Attack rates and food supply

Males and females attacked prey more often in swamp habitats than in levees, indicating a greater availability of food resources. Food supply may be an important component of habitat quality, and partly determine breeding success. Greater reproductive success of birds breeding in swamps resulted from larger clutch and brood sizes, rather than higher frequency of double-broods or lower nest predation (see Chapter 2). Clutch size and fledging success increase in areas or years of increased food supply for many passerines (reviewed in Martin 1987, Blancher and Robertson 1987, Rotenberry and Wiens 1991, Frey-Roos *et al.* 1995, Dias and Blondel 1996, Brodmann *et al.* 1997b, Seki and Takano 1998). Variation in food supply is therefore a plausible explanation for differential reproductive success of prothonotary warblers on the lower Roanoke River. The evidence in my study for variation in food supply (greater attack rates in swamps) is consistent with available evidence of habitat-specific demography in this system (see Chapter 2).

Birds may adjust clutch sizes according to their perceived ability to raise a brood in a habitat of a particular quality (Perrins and Moss 1975, Högstedt 1980). To test the hypothesis

that birds adjust clutch size to habitat conditions, Siikamaki (1995) moved nest boxes of pied

flycatchers (*Ficedula hypoleuca*) during nest building. Experimental nests were moved from

deciduous edges (preferred habitat) to coniferous edges (non-preferred habitat). Pairs nesting in

boxes that were moved from high to low quality habitat laid smaller clutches than control pairs,

whose nests were moved within high quality habitat. Siikamiki's (1995) study provided direct

evidence of the effect of territory quality on clutch size.

Evidence of the importance of food for clutch size comes from experiments that

employed supplemental food. Breeding females provided with supplemental food lay bigger

clutches than non-supplemented females (Aparicio 1994, Schoech 1996, Soler and Soler 1996).

Greater food availability also results in greater fledging success (e.g. greater mass and number of

fledglings, or greater proportion of nests producing at least one fledgling) (Siikamaki 1998,

Whittingham and Robertson 1994).

Other studies of prothonotary warblers have observed changes in foraging ecology in

response to proximate factors. Petit *et al*. (1990a, 1990b) conducted extensive studies on

foraging ecology of prothonotary warblers during the breeding season, and provide evidence that

this species makes strong behavioral responses to proximate factors, including prey abundance

and distribution. They evaluated differences between the sexes and among stages of the nest

cycle using data on foraging locations, substrates, and maneuvers. There were significant

differences between the sexes in several aspects of foraging ecology (height, substrate, etc. Petit

et al. 1990b). In addition, males and females both altered their food exploitation strategy during

prenestling and nestling periods (Petit *et al.* 1990b). Petit *et al.* (1990b) suggest that the parallel

shift of males and females demonstrates a behavioral response to temporal variation in proximate

factors. The primary behavioral response in the present study is spatial rather than temporal. The birds adjusted their attack rate in response to spatial variation in prey and abundance.

Search speed and effects of vegetation on foraging opportunities

The search speed of foragers did not vary with habitat (Fig. 3.1). Males and females changed perches, using hops or flights, about 15 times per min in both levees and swamps. Based on foraging theory, mean search time per prey type should be less in food-rich habitats. Mean search time is influenced by search speed and overall prey abundance, however. Birds foraging in swamp habitats appear to experience lower mean search time due to greater food abundance. One might expect birds foraging in levees to increase search speed, in order to decrease mean search time, but my results provide no evidence of any increase in search speed. Foragers may be under energetic or physiological constraints whereby increased speed would increase the energetic cost of foraging or decrease foraging efficiency. Risk of predation may also represent a foraging cost that would increase with increased speed or conspicuousness (Martin 1987, Martin 1992, Schmidt 1999). Individuals apparently possess the behavioral flexibility to adjust foraging speed (Ehlinger 1989), because males feeding fledglings searched faster than males that were not feeding fledglings. This behavioral response to fledglings suggests that physiological constraints are not operating. If risk of predation is a cost of foraging, it may be offset by benefits of foraging for offspring.

Mean estimates of foraging variables in my study are consistent with previous research on Prothonotary warblers and other warblers (e.g. Robinson and Holmes 1982, Robinson and Holmes 1984, Wiedenfeld 1992, Lovette and Holmes 1995). Prothonotary warblers in Panama

during the nonbreeding season attacked prey about 3 times per min and moved (hops plus

flights) about 18 times per min (Morton 1980). Corresponding estimates from my study are

about 2-3 attacks and 15 moves per min. Morton (1980) described foraging behaviors of

Prothonotary warblers during the nonbreeding season as diverse, as they included foraging from

dead leaves and taking nectar. In contrast, the exploitation strategy during the breeding season is

relatively simple; gleans often comprise about 80% of all foraging maneuvers (Petit *et al.* 1990b,

Petit *et al.* 1990a, this study).

Vegetation structure and plant species composition, in addition to food resources,

influence foraging tactics and capture success of foliage-gleaning birds (Robinson and Holmes

1984, Brodmann *et al.* 1997a). However, in an observational study of foraging behavior, it is

difficult to distinguish between effects of prey abundance and effects of vegetation structure and

composition. Arthropod abundance varies among tree species, and birds show tree-species

preferences when foraging (Holmes and Robinson 1981). Furthermore, exploitation strategies

and foraging success are influenced by the distribution of foliage within a plant (Robinson and

Holmes 1984). Thus, prey abundance and distribution, vegetation structure, and plant species

composition interact to create unique "foraging opportunities" which vary among bird species

(Holmes and Schultz 1988, Robinson and Holmes 1984). Nevertheless, whether attack rates are

greater in swamps due to vegetation features or overall prey abundance is inconsequential.

Warblers appear to consume more prey per unit time in swamps than in levees, and this may

have important consequences for fitness of individuals and habitat quality.

In conclusion, variation in prothonotary warbler density and reproductive success

between levees and swamps may be caused by variation in food resources. My results suggest

that appropriate measures of foraging behavior are sensitive to differences in foraging ecology

that may well provide insight to habitat quality, especially when combined with prey sampling. It is not possible to measure prey availability by prey-sampling alone (Holmes and Schultz 1988, Hutto 1990a). We should therefore combine behavioral approaches and arthropod sampling to maximize the power of inferences about food-based habitat selection and spatial structure of bird populations.

Acknowledgments

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Table 3.1. Robust general linear model analysis of attack rates and search speed as a function of habitat (levee or swamp) and nesting stage (incubation, nestling, recently fledged young, no nest). Parameter estimates (β) from statistical models are evaluated using t tests.

	Attack rate (attacks/min)				Search speed (moves/min)			
	β	SE	t	P	β	SE	t	P
Females (n = 32)								
Habitat	0.042	0.005	8.86	0.071	0.035	0.006	5.44	0.116
Nesting Stage	0.001	0.002	0.64	0.637	0.013	0.002	6.25	0.101
Males (n = 66)								
Habitat	0.037	0.002	15.20	0.042	0.017	0.003	5.44	0.116
Nesting Stage	-0.004	0.001	-4.07	0.154	-0.015	0.001	-11.55	0.055

Table 3.2. Log-linear models for type of attack (glean or aerial) and

locomotion (hop, short flight, long flight).

	df	χ^2	P
Type of Attack (n = 483 attacks)			
Habitat[a]	1	3.97	0.046
Sex	1	2.65	0.104
Nesting stage[b]	1	10.28	0.001
Likelihood-ratio test	4	7.04	0.134
Type of Locomotion (n = 2460 moves)			
Habitat[a]	2	3.53	0.171
Sex	2	0.39	0.821
Nesting stage[b]	2	4.78	0.092
Likelihood-ratio test	8	13.33	0.101

[a]levee or swamp

[b]recently fledged young or no active nest

Table 3.3. Robust general linear model analysis of foraging effort as a function of habitat (levee or swamp) and stage of nest cycle (incubation, nestling, recently fledged young, no nest). Foraging effort is proportion of total time budget. Parameter estimates (β) are evaluated using t tests.

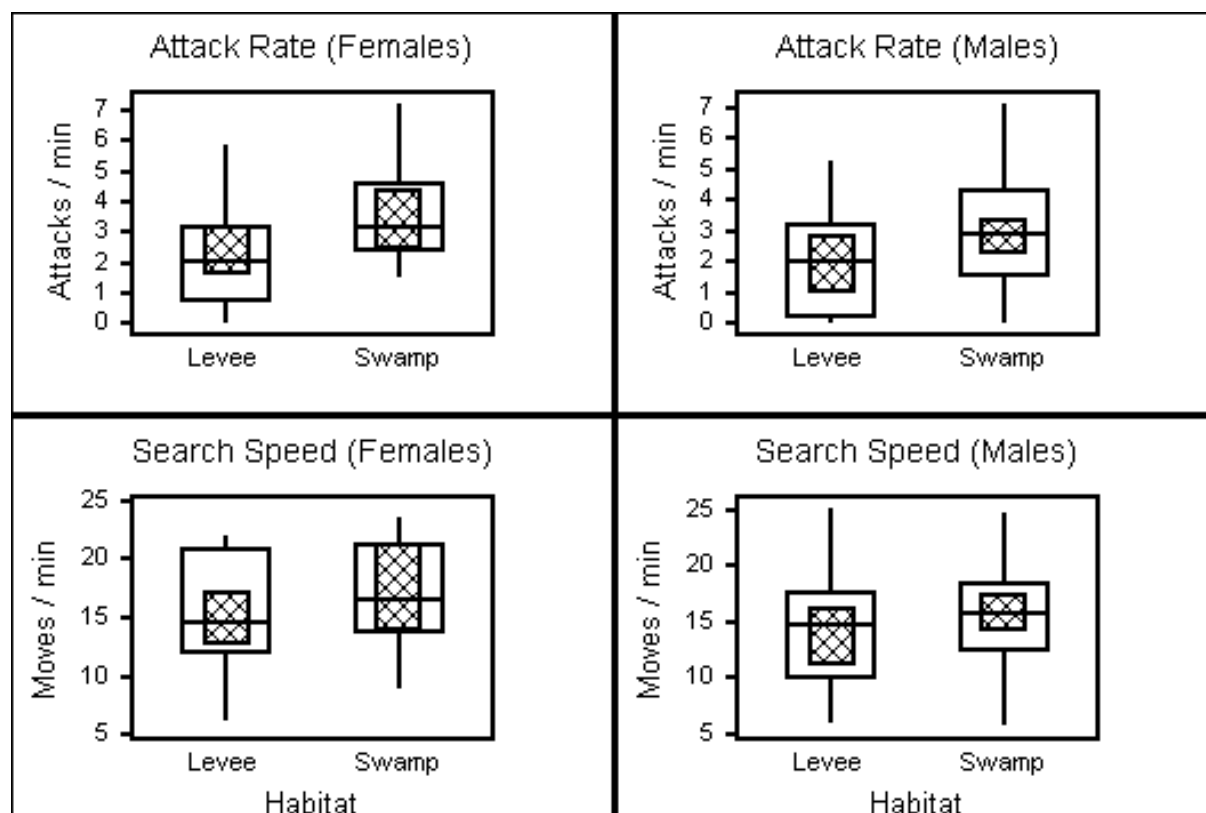|	β	SE	t	P
Females (n = 32)				
Habitat	-0.194	0.013	-14.98	0.042
Nesting stage	0.0	0.004	0.0	1.0
Males (n = 72)				
Habitat	0.114	0.012	9.44	0.067
Nesting stage	-0.016	0.004	-21.91	0.029

Figure 3.1. Attack rate (upper boxes) and search speed (lower boxes) of males (n = 66) and

females (n = 32) foraging in levee and swamp habitats. Each box-plot depicts the median

(horizontal line), 95% confidence interval for the median (small, cross-hatched box), the

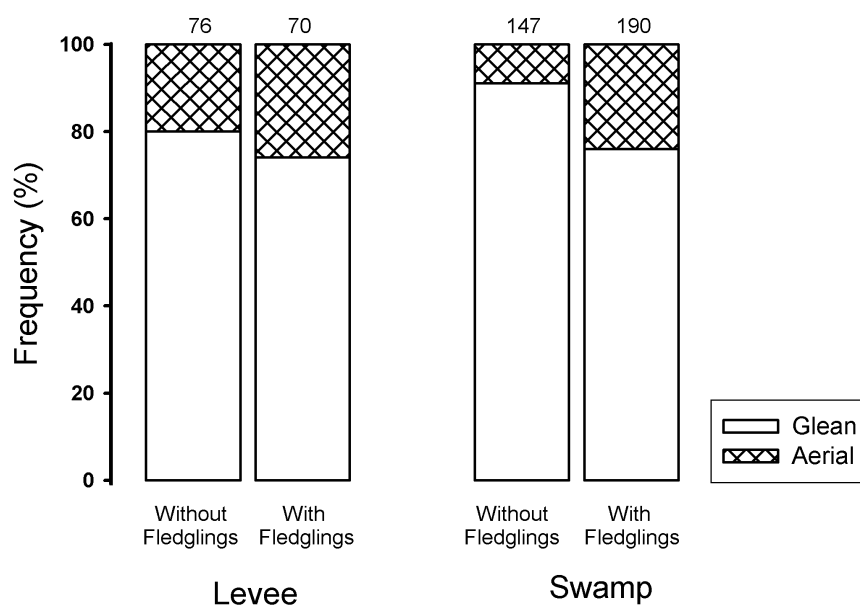interquartile range (large, open box), and the range (whiskers).

Figure 3.2. Relative proportions of gleans (open bar) and aerial attacks (cross-hatched bar) in two habitats and two stages of the nest cycle. Males and females are pooled because results indicated no difference between the sexes (see Results). Sample sizes (total no. foraging moves) are included above each bar.
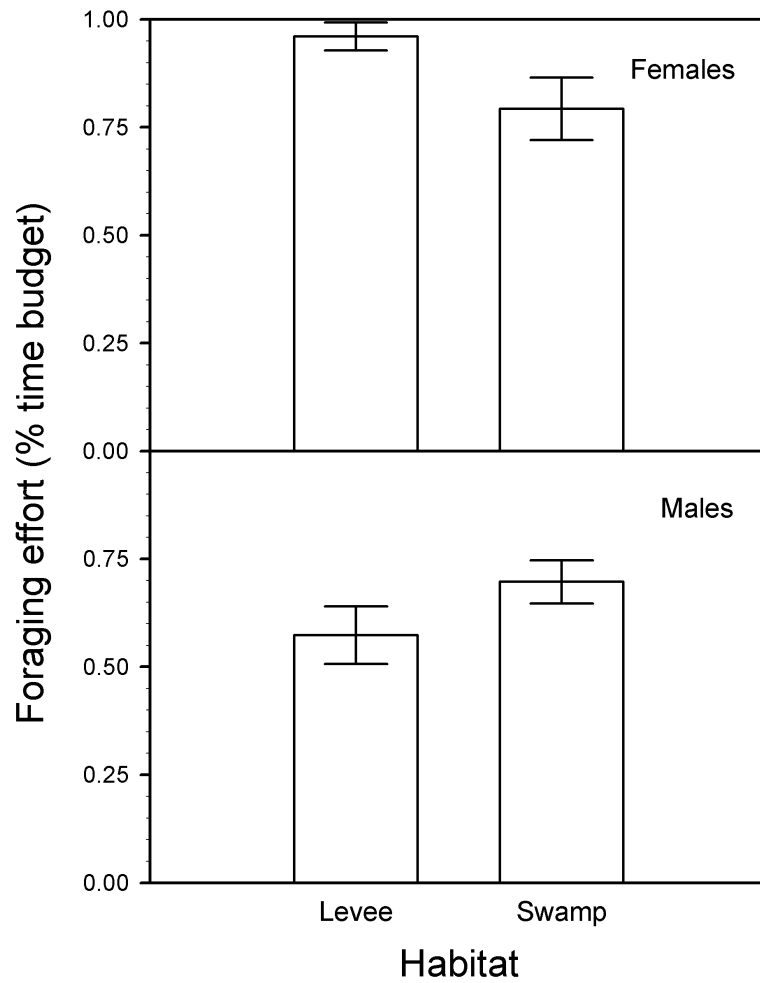
Figure 3.3. Foraging effort of males (n = 72) and females (n = 32) in levee and swamps.

Foraging effort is the mean proportion of total time budget devoted to foraging (± SE).

CURRICULUM VITAE

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M.S., Wildlife Biology, 1994 (Minor: Experimental Statistics)
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Thesis: Ecophysiology of shorebirds during winter and
migration at South Island, South Carolina
Advisor : Dr. Susan M. Haig

B.S., Wildlife Biology, 1986
Department of Wildlife and Fisheries Biology
University of Vermont, Burlington, Vermont

Research Interests: Avian population dynamics, bird-habitat relationships, animal behavior, conservation biology, behavioral ecology, animal migration

Research and Professional Experience :

1994-   *Graduate Research Assistant*, Department of Biology, Virginia Tech, Blacksburg, VA. Dissertation Research: Population ecology, habitat relationships, and foraging behavior of forest birds breeding in bottomland hardwood forests.

1991-1994   *Graduate Research Assistant*, South Carolina Cooperative Fish and Wildlife Research Unit, Clemson University, Clemson, South Carolina. Investigated population biology and stopover ecology of migratory shorebirds in partial fulfillment for M.S. degree. Coordinated a mark/recapture program of winter resident and spring migrant shorebirds investigating physiological responses influencing overwinter survival and testing hypotheses regarding the evolution of

migration in Nearctic-Neotropical sandpipers.

1990 - 1991   *Data Coordinator*, Western Hemisphere Shorebird Reserve Network, Manomet Bird Observatory, Manomet, Massachusetts. The Western Hemisphere Shorebird Reserve Network is an international cooperative program to conserve wetland areas critical to the conservation of migratory shorebird populations. Primary duties were managing a biological database for major staging areas in the Americas, coordinating an international marking scheme, advising and corresponding with researchers and field observers, maintaining a color mark sighting database, and supervising Latin American cooperators.

1989 - 1991   *Data Analyst/SAS Programmer*, International Shorebird Surveys, Manomet Bird Observatory. This program has produced the largest existing database on the abundance and distribution of New World shorebirds. Responsibilities included complete analyses for two computer investigations funded by the National Fish and Wildlife Foundation and the U. S. Fish and Wildlife Service.

1989 - 1990   *Research Biologist*, Manomet Bird Observatory. Assisted principal investigators in projects such as the Foraging Ecology of Roseate Terns (1990), Population Ecology of Osprey (1989), and Migration Ecology of Semipalmated Sandpipers at Plymouth Beach, Massachusetts (1989-1990).

1989 - 1991   *Microcomputer Systems Manager*, Manomet Bird Observatory. Responsible for maintenance of all Manomet Bird Observatory microcomputers, requiring an advanced knowledge of DOS, computer hardware and many popular software packages. Entailed writing software documentation, instructing MBO staff and students in the use of word processors, spreadsheets and data management programs and upgrading and repairing computer systems.

1988   *Field Biologist*, Southeast Farallon Island, Point Reyes Bird Observatory, Stinson Beach, CA. A National Wildlife Refuge located 27 miles off the coast of California, Southeast Farallon Island hosts the largest breeding seabird colonies south of Alaska. All projects involved monitoring populations of banded known-age individuals throughout the breeding cycle, including nest checks on hundreds of Western Gulls, behavioral watches and foraging ecology research of Brandt's Cormorants and the collection of productivity data from Cassin's Auklets, among other projects.

1986 - 1988   *Research Assistant*, Lloyd Center for Environmental Studies, South Dartmouth, MA. Principal investigator, Breeding Biology of Piping Plovers in Bristol Co., MA (1986-1987). Principal investigator, Winter Ecology of American Black Ducks at a Massachusetts Estuary (1987). Research Assistant, Avian Community Dynamics at Allens Pond Estuarine Complex (1986-1988).

Teaching Experience:

1996, 1998, 2000   *Teaching Assistant*, Principles of Biology Laboratory for Biology Majors, Department of Biology, VPI & SU, Blacksburg, Virginia.

1998   *Teaching Assistant*, Ornithology, Department of Biology, VPI & SU, Blacksburg, Virginia.

1989 - 1991   *Teaching Assistant*, Field Biology Training Program, Manomet Bird Observatory, Belize, Puerto Rico, and Massachusetts. Supervised undergraduate field studies of shorebirds in Puerto Rico, tropical forest birds in Belize, and Osprey in Massachusetts.

Professional Associations :

American Ornithologists' Union	1993
Cooper Ornithological Society	1995
Wilson Ornithological Society	1995
Association of Field Ornithologists	1995
Ecological Society of America	1996

Awards :

AOU Marcia Brady Tucker Travel Award	1993
EM-SCAN Calibration Research Award	1994

Service:

Manuscript Reviews for *The Auk*, *The Condor*, and *Wilson Bulletin*.

Peer-reviewed Publications:

Lyons, J. E. and S. M. Haig. 1995. Estimation of lean and lipid mass in shorebirds using total body electrical conductivity. Auk 112(3):590-602.

Lyons, J. E. and S. M. Haig. 1995. Fat content and stopover ecology of spring migrant Semipalmated Sandpipers in South Carolina. Condor 97:427-437.

Reports and Abstracts:

Lyons, J. E., J. R. Walters, and J. A. Collazo. 1998. Continued studies of population dynamics and habitat relationships of breeding birds in bottomland hardwood forests along the Roanoke River in North Carolina: Project final report. Department of Biology, Virginia Polytechnic Institute and State University, Blacksburg, Virginia.

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Poole, A.F. and J. E. Lyons. 1991. Status and assessment of the birds of Buzzards Bay, Massachusetts: an historical and present overview. In *Living Resources of Buzzards Bay*, J. Costa, ed. Buzzards Bay Project, New Bedford, Massachusetts.

Harrington, B. A. and J. E. Lyons. 1990. On the importance of wildlife areas in the United States to shorebirds migrationg east of the 105th longitudinal lines. Report, National Fish and Wildlife Foundation, Washington, D.C.

Lyons, J. E. 1988. Aspects of the breeding biology of Piping Plovers in Bristol Co., Massachusetts. Lloyd Center Research Contribution 88-2.

Melvin, S., L. MacIvor, J. E. Lyons, and J. Swensen. 1987. Impacts of predation on Piping Plover productivity in Massachusetts: a preliminary assessment. Proceedings of the Northeast Fish and Wildlife Conference, Boston, MA.

Manuscripts in Preparation:

Lyons, J. E. Habitat-specific demograpy, breeding site fidelity, and potential population regulation in a territorial, migratory passerine.

Lyons, J. E. Habitat-specific foraging behavior of breeding Prothonotary Warblers: deducing habitat quality.

Lyons, J. E. Nest success of forest birds at edge and interior locations in a bottomland hardwood forest.

Lyons, J. E. Effects of forest structure and floristics on avian assemblages in a bottomland hardwood mosaic.

Papers at National Meetings:

Lyons, J. E. 1999. Foraging behavior of Prothonotary Warblers in two habitats: attack rate and search speed in levee and swamp forest. 1999 Annual Meeting of the American Ornithologists' Union, Ithaca, NY

Lyons, J. E. 1998. Habitat specific demography and population dynamics of a migratory songbird. 1998 Annual Meeting of the Ecological Society of America, Baltimore, MD, 3 August 1998.

Lyons, J. E. 1998. Reproductive success and habitat selection of Prothonotary Warblers: potential links between individual behavior and population dynamics. 1998 Annual Meeting of the American Ornithologists' Union, St. Louis, MO, 12 April 1998

Lyons, J. E. 1996. Local population size estimation at a migratory stopover site. Migratory Shorebird Ecology and Management Workshop sponsored by the U. S. Fish and Wildlife Service National Training and Education Center. 8 May 1996, Pawley's Island, SC.

Lyons, J. E. 1995. Influence of date and body condition on stopover decisions of spring migrant Semipalmated Sandpipers in South Carolina, USA. 1995 Annual Meeting of the American Ornithologists' Union, 17 August 1995, Cincinnati, Ohio.

Lyons, J. E. 1993. Estimation of lean and lipid mass in live birds: total body conductivity (TOBEC) and scaled body measurements. 1993 Annual Meeting of the American Ornithologist's Union, 14 June 1993, Fairbanks, AK.

Papers at Regional Meetings, Seminars, and Invited Presentations:

Lyons, J. E. 1998. Breeding biology of the Prothonotary Warbler in the lower Roanoke River bottomlands. 1998 Annual Meeting of the Virginia Society of Ornithology, Mountain Lake, VA. 16 May 1998

Lyons, J. E. 1998. Habitat relationships and population dynamics of breeding birds in the lower Roanoke River basin, NC. Department of Biology Seminar, Virginia Polytechnic Institute and State University, Blacksburg, VA.

Lyons, J. E. 1998. Conservation and management of birds breeding in the bottomland hardwoods of the lower Roanoke River, North Carolina. New River Valley Bird Club Meeting, 4 March 1998

Lyons, J. E. 1995. Bird populations studies in bottomland hardwood forests of the Roanoke River. Annual Meeting of Geogia-Pacific/The Nature Conservancy Cooperative Research Program, Windsor, North Carolina, 21 May 1995.

Lyons, J. E. 1987. Piping Plovers in Southeastern Massachusetts: conservation and management of an endangered species. Lloyd Center Lecture Series, South Dartmouth, MA.

Lyons, J. E. 1987. Birds of Allens Pond: specialties of a coastal stopover. Presentation for the Paskamansett Bird Club, South Dartmouth, MA.