AVIAN NEST SURVIAL AND BREEDING DENSITY IN COTTONWOOD PLANTATIONS AND NATIVE FOREST FRAGMENTS IN SOUTHEAST MISSOURI

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Doctor of Philosophy

By

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The undersigned, appointed by the dean of the Graduate School, have examined the dissertation entitled

AVIAN NEST SURVIAL AND BREEDING DENSITY IN COTTONWOOD PLANTATIONS AND NATIVE FOREST FRAGMENTS IN SOUTHEAST MISSOURI

presented by Michael Shane Pruett,

a candidate for the degree of doctor of philosophy,

hereby certify that, in their opinion, it is worthy of acceptance.

Dr. Frank Thompson

Dr. Mickey Heitmeyer

Dr. John Faaborg

Dr. Mark Ryan

Dr. Mark Ellersieck

DEDICATION

To my family, for all you have done, and do.
Thank you.

PARENTS
Ken and Linda

who have supported every decision I've made,
who have allowed me to create my own successes and measure my own failures,
who have provided structure, and values, and love

and who have, I believe, never doubted me.
I love you.

WIFE
Grechen

who has believed in me,
who has loved me unconditionally and unreservedly,
who has given me joy and laughter,

and who stands by me in all I do.
shmily

DAUGHTER
Allaine

who has my whole heart.

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ABSTRACT

I compared nest survival and breeding density between native bottomland forest and cottonwood (*Populus deltoides*) plantations over a three-year period for Acadian Flycatcher (*Empidonax virescens*), Prothonotary Warbler (*Protonotaria citrea*), and Indigo Bunting (*Passerina cyanea*). Nest survival was similar in both forest types and varied throughout the season for all species. Acadian Flycatcher nest survival increased and parasitism by Brown-headed cowbird (*Molothrus ater*) decreased with increasing percent forest cover. Indigo Bunting nest survival was negatively associated with distance to edge and probability of parasitism decreased in larger patches. I used video cameras to record songbird nests in both forest types. Snakes and birds, including Brown-headed cowbirds, were nest predators.

I compared unadjusted abundance estimates from point count data to multiple model-based estimates. Densities of Acadian Flycatcher and Prothonotary Warbler were higher in native forest. Indigo Bunting densities were higher in plantations, but significance of the difference depended on the method used. Methods incorporating multiple time intervals and the full encounter history of each individual provided more precise estimates than traditional removal methods or distance methods.

Chapter 1 - Songbird Nest Survival And Parasitism In Plantation And Native Forests In The Mississippi Alluvial Valley.

Introduction

Concern over the decline of some Neotropical migratory birds has generated interest in determining what factors are most important for the maintenance of viable populations (Burdick et al. 1989; Robbins et al. 1989; Askins et al. 1990; Faaborg et al. 1995; Donovan and Flather 2002). Habitat loss and fragmentation are correlated with the decline of some forest nesting birds in North America (Robbins et al. 1989; Askins et al. 1990; Donovan and Flather 2002). Fragmentation effects may be more pronounced with increasing fragment isolation or when fragmentation results in two distinctly different adjacent habitats (i.e. forest and agriculture) (Chalfoun et al. 2002a; Thompson et al. 2002). In southeast Missouri, bottomland hardwood (BLH) forests of the Mississippi Alluvial Valley (MAV) have been reduced to approximately 6% of their original extent (Twedt and Loesch 1999). Only one forest patch in the Missouri portion of the MAV is larger than 4,000 ha, the minimum size suggested by Mueller et al. (1999) for maintaining a viable population of breeding songbirds in the MAV. The mean patch size is 23 ha, and 98% of the 2483 patches were < 1012 ha (Twedt and Loesch 1999).

The combination of floods, fluctuating agricultural markets, and concern over the extreme changes to the Mississippi river bottomlands and associated impact on wildlife populations influence interest in restoration efforts throughout the MAV (Mueller et al. 1999). In some areas the Army Corps of Engineers and other land management agencies are working to utilize remaining waterways and land acquisition to increase forest cover and connectivity.

There is also interest in restoring some of the natural hydrological periodicity to the system to reintroduce more natural hydrogeological functioning (i.e. sediment trapping, filtering of nutrients) (Brown et al. 1999). Recently, agricultural fields, particularly those in flood prone areas, have been utilized for production of pulp wood through afforestation with cottonwood monocultures. Development of mature forest characteristics (i.e. vertical structure, canopy closure) and subsequent colonization by forest birds can be hastened by planting fast growing species (Twedt and Portwood 1997; Schoenholtz et al. 2001). If plantations represent suitable habitat, forest-dependent species may benefit directly due to increased breeding habitat and indirectly (in native forest remnants) from increased forest cover in the landscape that may mitigate fragmentation effects (Robinson et al. 1995). Afforestation and plantation forestry therefore may offer an opportunity to benefit breeding birds, while continuing to provide an economic return to landowners (Twedt and Portwood 1997).

The MAV Migratory Bird Planning Group convened to coordinate MAV habitat restoration efforts for the conservation of avian biodiversity (Brown et al. 1999). They outlined the most efficient means for increasing habitat quantity and quality, given current conditions (i.e. the distribution and size of existing forest patches) (Twedt et al. 1999). The goals were state specific, described the targeted number of patches of different sizes, and reflected the fact that the greatest gains could likely be made in the southern portion of the MAV. Twedt et al. (1999) argued the need to evaluate landscape changes in the MAV for meeting the goal of maintaining viable bird populations. Necessary data includes measures of population parameters such as density, nest survival, parasitism and predation rates in the current forest patches for comparison with other studies to determine whether extrapolations from those studies to this landscape are warranted. Further, data is needed to confirm the appropriateness not only of extrapolation from other populations of a given species, but across species as well (Twedt et al. 1999).

We determined nest survival and brood parasitism levels of migrant, forest nesting, passerine birds in remnant bottomland hardwood and cottonwood plantation forests in southeastern Missouri. We predicted that birds in native forest would have greater nest survival than birds in plantations (Twedt et al. 2001) and that nest survival would be greater in larger forest patches, and in areas containing a higher percentage of forest in the landscape. We predicted that nest survival would vary temporally (Grant et al. 2005). We predicted that parasitism would be higher in smaller fragments and in landscapes with less forest cover. We assumed that parasitism would increase rapidly early in the breeding season, and then decline throughout the summer. Broader comparisons of our findings to others in upland Midwestern forests and other bottomland systems across the southern U.S. will provide both regional and ecosystem based contexts for understanding the current functional value of this system to breeding birds.

Methods

STUDY AREA

We conducted this study during the breeding seasons of 2004-2006 in the remnant bottomland hardwood forests and plantation forests of the New Madrid floodplain in the southeastern Missouri portion of the MAV (Mississippi and New Madrid Counties) and on two small islands comprising portions of the Kentucky counties of Carlisle and Hickman.

Study areas were on private lands and Donaldson Point and Ten Mile Pond Conservation Areas (Missouri Department of Conservation) and Big Oak Tree State Park (Missouri Department of Natural Resources).

This area was historically extensively forested by temperate deciduous flood forest and was subject to periodic inundation from the Mississippi river. Vegetative cover reflected the microtopography and flood tolerance of the individual species, and resulted in very high levels of diversity . Remnant BLH forests on the study sites are characterized by a mix of deciduous tree species including oaks (*Quercus* spp.), willows (*Salix* spp.), hickories (*Carya* spp.), ash (*Fraxinus* spp.), maples (*Acer* spp.), sugarberry (*Celtis laevigata*), and American sycamore (*Platanus occidentalis*). The remaining forest, excepting a small section of Big Oak Tree State Park, has been harvested in the past and is in various stages of secondary growth and development. Cottonwood (*Populous deltoides*) is the most commonly planted tree in plantations (M. S. Pruett pers. obs). The study area is bounded on the east by the Mississippi river. Row cropping is now the predominate land use. Major crops include soybeans, corn, millet, and sunflowers.

Study plots were selected to represent the range of forest cover levels and most were initially used in the context of a larger faunal study (Papon 2002). Sixteen four-mi^2 blocks were randomly selected from over 250 possible blocks in the Missouri MAV; five had < 8%, four had 8-20%, and seven had > 20% forest cover. We used 10 of these sites in the first year and nine in the remaining years. Within these four mi^2 blocks, the sizes of the actual study plots (forest patches) are varied and depend on pre-existing forest conditions, whether natural or planted.

NEST SUCCESS

We focused on three common species: Acadian Flycatcher (*Empidonax virescens*), Prothonotary Warbler (*Protonotaria citrea*), and Indigo Bunting (*Passerina cyanea*). We selected these species because they are numerous, easily observable, and because there is considerable literature on their nest success in other systems for comparison.

We located nests by actively searching likely areas, and observing adult bird behavior to locate nests during all stages. While we attempted to locate nests during the building stage, most nests were found during laying, incubation, and nestling periods. We determined a nest's status either by visual inspection or by watching parental behavior at high nests. We marked the location of nests in the field with flagging at a distance greater than 10 m from the nest to reduce disturbance to the nest or adults and to reduce the likelihood of a predator using flags as a cue. During each visit we recorded the nest ID, study plot, date, location description, species, nest stage, presence or absence of water under the nest substrate, nest contents, including presence of Brown-headed Cowbird eggs or nestlings and any other comments relevant to the nest's status. We attempted to revisit nests at 3-4 day intervals and then daily near the end of the nest cycle to increase the certainty of determining nest fate. We avoided flushing females if possible, particularly if the nest stage was known or could be inferred (e.g. a female observed on the nest early in incubation, or feeding nestlings).

We monitored nests that were too high for direct observation with a combination of binocular observation near the nest and an extensible pole mounted with either a mirror or small camera. The camera pole was equipped with a microvideo camera wired to a small battery pack and viewer on the ground. The mirror pole was equipped with a simple, adjustable angle mirror, and was viewed with binoculars. The poles allowed us to accurately monitor the contents of nests up to at least 15.25 m.

Nests were considered successful if at least one young fledged regardless of whether the bird was host or Brown-headed Cowbird. When an empty nest was found on the last visit, and fledging was anticipated or possible, the area was searched, sometimes over consecutive days, in an attempt to verify fledging. In instances where no fledglings were found, nests were still considered successful under the following conditions: the nest edge was depressed as by nestlings sitting on the rim just prior to fledging, fecal material was evident on vegetation or ground beneath nest or nest branch, parental behavior indicated potential for fledgling care, even if there was a subsequent nest attempt. Predation was assumed when there was damage to the substrate or nest consistent with depredation, when the nestlings were too young to have forced fledged, or when both parents were found engaged in a renest attempt following nestling disappearance with no indication that either was concurrently caring for fledged young. We excluded observations for intervals where the fate of the nest during that interval could not be determined.

As soon as possible after a fledge or failure the nest characteristics were measured (Burhans and Thompson 1998). Measurements included nest height (measured from nest bottom to ground or water surface), nest substrate identity, substrate diameter at breast height (DBH), concealment data (six measures: each cardinal compass point, above, and below) (Nudds 1977; Noon 1981; Ortega et al. 2002), mean angular canopy cover (2 spherical densitometer readings: facing N and S with back to nest) (Nuttle 1997; Twedt et al. 2001), distance to main stem, distance to edge, and UTM coordinate location (via portable GPS module). The distance to edge was measured directly if nearby, by pacing if visible but at greater distance, and during analysis (via GIS) if the nearest edge was not known. Diameter at breast height and identity of all trees within a 5.64 m radius circle was recorded as a measure of forest structure in the immediate nest vicinity.

LANDSCAPE METRICS

We calculated landscape metrics using ArcGIS 9 and Fragstats (Environmental System Research Institute, Redlands, California). We assigned land cover type by digitizing recent orthophotos (Missouri Spatial Data Information Service website. 2007. http://www.msdis.missouri.edu/datasearch/ThemeList.jsp (Sept. 2007)) using a minimum mapping unit of 10 m and then rasterized the map using a 10-m cell size. We assigned each polygon one of five cover types: native forest, plantation forest, open, developed, and water. We calculated landscape metrics at one km (314 ha) and five km (7854 ha) radii around each nest (Knutson et al. 2004). We chose these radii because at larger radii statistics for the sites become homogeneous because they are predominately agricultural land. We calculated percent forest cover of each forest type as well as total percent cover of forest, water, developed, and agriculture land uses. We also calculated the ratio of forest to agriculture, distance to edge, distance to water, patch size, and density of edges. Here we report only the 5 km radius results because 1 km results were generally consistent in terms of model selection results and strength of effects.

STATISTICAL ANALYSES

Nest Survival. We used the logistic exposure method (Shaffer 2004) to model daily nest survival of each species as a function of temporal and habitat variables in PROC GENMOD (SAS Version 9.1, SAS Institute, Cary, North Carolina). This approach reduces bias potentially associated with earlier methods (i.e. Mayfield) by assuming homogeneity among nests with the same values of explanatory variables, but not that survival itself must be homogeneous among nests (Shaffer 2004).

We evaluated models (described below) for each species using Akaike's Information Criteria for small sample sizes (AIC_c) to rank the models from most to least supported (Burnham and Anderson 2002). The best model given the set of *a priori* models has the lowest value of AIC_c and represents a tradeoff between the highest logL and the fewest parameters necessary to achieve reasonable fit. Before evaluating candidate models we evaluated the global model for evidence of lack of fit by examining the overdispersion parameter (goodness of fit χ^2 / d.f.; Burnham and Anderson 2002). Values that deviate substantially from one indicate a poor fit of the model under consideration. We also examined models for multicollinearity and excluded variables if tolerance values were > 0.40 (Allison 1999). The models are ranked by their weights (w_i) which represent the probability of the model relative to the other models in the *a priori* model set. We compared closely ranked models by evaluating evidence ratios and ΔAIC_c values (Burnham and Anderson 2002).

We first modeled nest success of each focal species as a function of temporal variables. We then selected the best temporal model for each species and included those variables in all subsequent habitat models for that species (Grant et al. 2006) (Table 1-1, Table 1-2). This approach allowed us to control for important temporal variables while investigating potentially important habitat or landscape effects.

Table 1-1. Candidate temporal and habitat models used to evaluate hypothesized effects on nest survival of Acadian Flycatcher, Prothonotary Warbler, and Indigo Bunting in the Mississippi Alluvial Valley.

Temporal models	Habitat models
year	Height
stage	Patch + distedge, type
julian	cover5 + distwater
julian + $julian^2$	k5plaf + k5natf + distwater
julian + $julian^2$ + $julian^3$	Cbpara
year + stage	Height + patch + distedge, type
year + julian	Height + cover5 + distwater
year + julian + $julian^2$	Height + k5plaf + k5natf + distwater
year + julian + $julian^2$ + $julian^3$	Patch + distedge + type +cover5 + distwater
stage + julian	Patch + distedge + type + k5plaf + k5natf + distwater
stage + julian + $julian^2$	Height + patch + distedge + type
stage + julian + $julian^2$ + $julian^3$	Height + patch + distedge + type + k5plaf + k5natf + distwater
year + stage + julian	Height + cover5 + distwater
year + stage + julian + $julian^2$	Height + k5plaf + k5natf + distwater
year + stage + julian + $julian^2$ + $julian^3$	Patch + distedge + type +cover5 + distwater

Year = 2004, 2005, 2006, julian = day of year, height = nest height, patch = area of forest patch, type = plantation or native forest, cover5 = percent forest cover in 5 km radius circle, distwater = distance to water, distedge = distance to closest forest edge, cbpara = Brown-headed Cowbird parasitism, k5plaf = percent plantation forest in a 5 km radius, k5natf = percent native forest in a 5 km radius.

Table 1-2. Most supported candidate models (∆AICc < 2.0.) used to evaluate factors affecting nest survival of Acadian Flycatcher, Prothonotary Warbler, and Indigo Bunting in the Mississippi Alluvial Valley.

Model[a]	logL[b]	K[c]	ΔAIC_c[d]	w_i[e]
Acadian Flycatcher				
julian + julian^2	-271.322	3	0.000	0.279
julian + julian^2 + cover5 + distwater	-269.837	5	1.046	0.165
julian + julian^2 + parasitism	-271.218	4	1.798	0.114
Prothonotary Warbler				
julian + julian^2 + type	-121.547	4	0.000	0.54
Indigo Bunting				
Year + julian + julian^2 + julian^3	-309.468	6	0.000	0.157
Year + julian + julian^2 + julian^3 + height + patch + type + distedge	-305.729	10	0.592	0.117
Year + julian + julian^2 + julian^3 + height + patch + type	-306.768	9	0.650	0.114
Year + julian + julian^2 + julian^3 + cbpara	-308.957	7	0.992	0.096
Year + julian + julian^2 + julian^3 + height	-309.073	7	1.224	0.085
Year + julian + julian^2 + julian^3 + cover5 + distwater	-308.067	8	1.228	0.085
Year + julian + julian^2 + julian^3 + cover5 + distwater + height	-307.148	9	1.409	0.078
Year + julian + julian^2 + julian^3 + height + cbpara	-308.444	8	1.984	0.058

[a] Variable names are defined in Table 1.

[b] LogL = loglikelihood.

[c] K = number of parameters in the model.

[d] ΔAIC_c = adjusted AIC_c relative to the top model.

[e] w_i = Akaike weight, a measure of the relative support for each model.

We hypothesized variation in survival due to nest stage (Peak et al. 2004), year (Mahon and Martin 2006), and date (Grant et al. 2005) (Table 1-1). We expected daily nest survival to vary throughout the breeding season, and we modeled higher order terms of Julian date (Julian^2, Julian^3) to evaluate potential non-linear effects (Shaffer 2004; Grant et al. 2005). Models incorporating higher order terms also included all lower order terms (e.g. Julian^3 = Julian + Julian^2 + Julian^3).

We considered habitat variables representing effects at the nest or immediately around it, at the forest patch where the nest was found, and landscape effects in a 5 km radius around each nest. At the landscape scale we considered two competing models for our hypothesis that nest success increased with percent forest cover. The first model included the percent of forest cover and distance to water, while the second included the percent native forest cover plus the percent of plantation forest cover plus distance to water. The second model allowed us to evaluate the hypothesis that not only the amount of forest, but also how much of each exerts an influence on nest survival. We also hypothesized nest survival to be lower near permanent water sources because some nest predators have greater activity near water (Dijak and Thompson 2000). At the patch level, we predicted patch size (patch) (Hoover et al. 1995) and distance to edge (distedge) (Hoover 2006a) to be positively associated with nest survival, and we predicted higher survival in native than plantation forests (type) (Twedt et al. 2001). At the nest site we expected survival to increase with nest height (Wilson and Cooper 1998), and nests over water to have higher survival than nests over dry ground (flood) (Hoover 2006b). A final variable of interest was whether nest survival would be influenced by parasitism. We predicted that nests parasitized by the Brown-headed Cowbird would have lower survival than unparasitized nests (Donovan et al. 1995). We hypothesized that factors at one or more of these scales could affect nest survival so the *a priori* model set consisted of nest site, nest patch, and landscape models, and additive combinations of these, resulting in 18 habitat models for Acadian Flycatcher, 17 for Prothonotary Warbler, and 16 for Indigo Bunting (Table 1-1).

We produced model-averaged daily and period survival rates based on the complete model set as a function of supported covariates over their observed ranges while holding all effects of other covariates constant (Shaffer and Thompson 2007). Continuous covariates were held constant at their mean and categorical covariates were held constant at levels representing the proportion of observations in each category level, except for nest stage, which we set to represent the proportion of the nest cycle spend in each stage (Shaffer and Thompson 2007). We used species-specific nest period lengths from the Birds of North America (Petit 1999; Whitehead and Taylor 2002; Payne 2006) accounts for each species and other published information (Ehrlich et al. 1988) to compute period survival rates. We used model averaged (weighted) parameter estimates and associated standard errors to calculate odds ratios and their 95% confidence limits. The odds ratios allow direct comparison of the effects of categorical variables and comparison across the range of continuous variables (Shaffer and Thompson 2007).

Parasitism. We used logistic regression to model the probability of Brown-headed Cowbird parasitism for each species. We classified each nest as parasitized or non-parasitized based on the presence of cowbird eggs or young at any stage of the nest cycle. We modeled this binary response (parasitized or non-parasitized) as a function of the same temporal, landscape, nest patch, and nest site variables considered in the nest survival analysis and using the same model selection procedures. We hypothesized cowbird use of forested habitats was influenced by the same factors we considered for nest survival. For example, cowbirds are more common in landscapes of low forest cover (Robinson et al. 1995; Chace et al. 2005), and parasitism may be less likely to occur as vegetative density increases (Chace et al. 2005). As with the nest survival analysis, we first modeled parasitism as a function of temporal variables (year, Julian date, $Julian^2$, and $Julian^3$) and then carried the most important variables forward into the analysis of habitat parameters. Using procedures similar to the nest survival analysis, we produced model-averaged estimates of the probability a nest was parasitized as a function of supported covariates.

Results

Table 1-3. Mean, standard error, and range for covariates in the analysis of habitat effects on nest survival of Acadian Flycatcher, Indigo Bunting, and Prothonotary Warbler in southeastern Missouri.

Variables	Mean	SE	Min	Max
Acadian Flycatcher				
Nest Height (m)	7.04	0.23	0.57	16.15
Distance to water (m)	1330.05	119.05	1.00	5602.00
Distance to edge (m)	322.83	25.11	5.00	1461.00
% Native forest (5K)	19.72	0.86	5.93	39.84
% Plantation (5K)	7.17	0.66	0.00	21.70
Patch area (ha)	1042.12	75.28	68.17	2531.67
Prothonotary Warbler				
Nest Height (m)	3.11	0.23	0.60	10.11
Distance to water (m)	1539.14	209.11	7.00	5688.00
Distance to edge (m)	293.50	30.02	3.00	1286.00
% Native forest (5K)	15.76	0.84	5.96	39.96
% Plantation (5K)	7.54	1.04	0.00	22.26
Patch area (ha)	780.88	73.41	2.46	2531.67
Indigo Bunting				
Nest Height (m)	0.99	0.07	0.20	7.88
Distance to water (m)	1766.88	109.28	23.00	5593.00
Distance to edge (m)	290.48	23.13	0.00	1279.00
% Native forest (5K)	17.50	0.66	5.65	39.00
% Plantation (5K)	11.50	0.63	0.00	22.37
Patch area (ha)	897.66	138.81	68.17	27375.06

NEST SURVIVAL

Acadian Flycatcher. We monitored 150 Acadian Flycatcher nests for 852 nest-observation intervals. Ninety-eight nests were in native forest and 52 were in plantations. Seventy-two (48%) Acadian nests were depredated, and 61 (40.7%) nests fledged at least one chick. Four nests were depredated during the laying stage, 32 during incubation, and 35 during the nestling stage. In plantation forests, 25 of 52 nests (48.1%) were depredated, and in native forests 47 of 98 nests (48.0%) were depredated. Thirty-four nests were parasitized by Brown-headed Cowbirds.

Assessment of the overdispersion parameter of the global model (goodness of fit χ^2 / d.f. = 0.9437; Burnham and Anderson 2002) indicated no evidence of lack of fit. The most supported temporal model was the Julian^2 model ($w_i = 0.428$). It was also the most supported model in the habitat analysis ($w_i = 0.279$) (Table 1-2). The second most supported model included percent forest cover and distance to water and the third most supported model included parasitism (Table 1-2). All other models had low support, with $\Delta AIC_c > 2.0$ and Akaike weights < 0.1. The model averaged daily survival rate (DSR) of Acadian Flycatcher nests was 0.968 (0.957 – 0.977) resulting in overall period survival of 0.373 (0.260 – 0.486). Daily survival was highest in the beginning of the breeding season (late May), reached a low late in the season (second week of July), and began increasing again until the birds transitioned to post breeding movement (Figure 1-1A). Model-averaged odds ratios for percent forest cover, distance to water, and parasitism had confidence limits that overlapped 1 (no effect, Table 1-3), however examination of predicted nest survival as a function of percent forest indicated potentially meaningful effects. Period survival ranged from 0.338 to 0.409 in landscapes with 5% to 50% forest cover (Figure 1-2A).

Prothonotary Warbler. We monitored 78 Prothonotary Warbler nests for a total of 373 intervals. Fifty-one nests were in native forests, and the remaining 27 were in plantations. However, only three of the plantation nests were in natural cavities. The remainder were in nest boxes that were hung for a discontinued project. Due to the sparseness of natural nests in plantations, we included the results of artificial box nests in this analysis. Thirty-one (40%) Prothonotary Warbler nests fledged at least one chick, 14 (18%) in plantations, and 17 (22%) in native forest. Thirty-seven (47%) nests were depredated. Twenty-nine (37%) nests were depredated in native forests; four during laying, 12 during incubation, and 13 during the nestling stage. Of seven (9%) nest depredations in plantations, six occurred during the nestling stage, one occurred during the incubation stage, and all were associated with nest

Figure 1-1. Model averaged daily survival rate (DSR) and 95% CI of focal bird species by Julian date. (A) Acadian Flycatcher (ACFL). (B) Prothonotary Warbler (PROW). (C) Indigo Bunting (INBU).

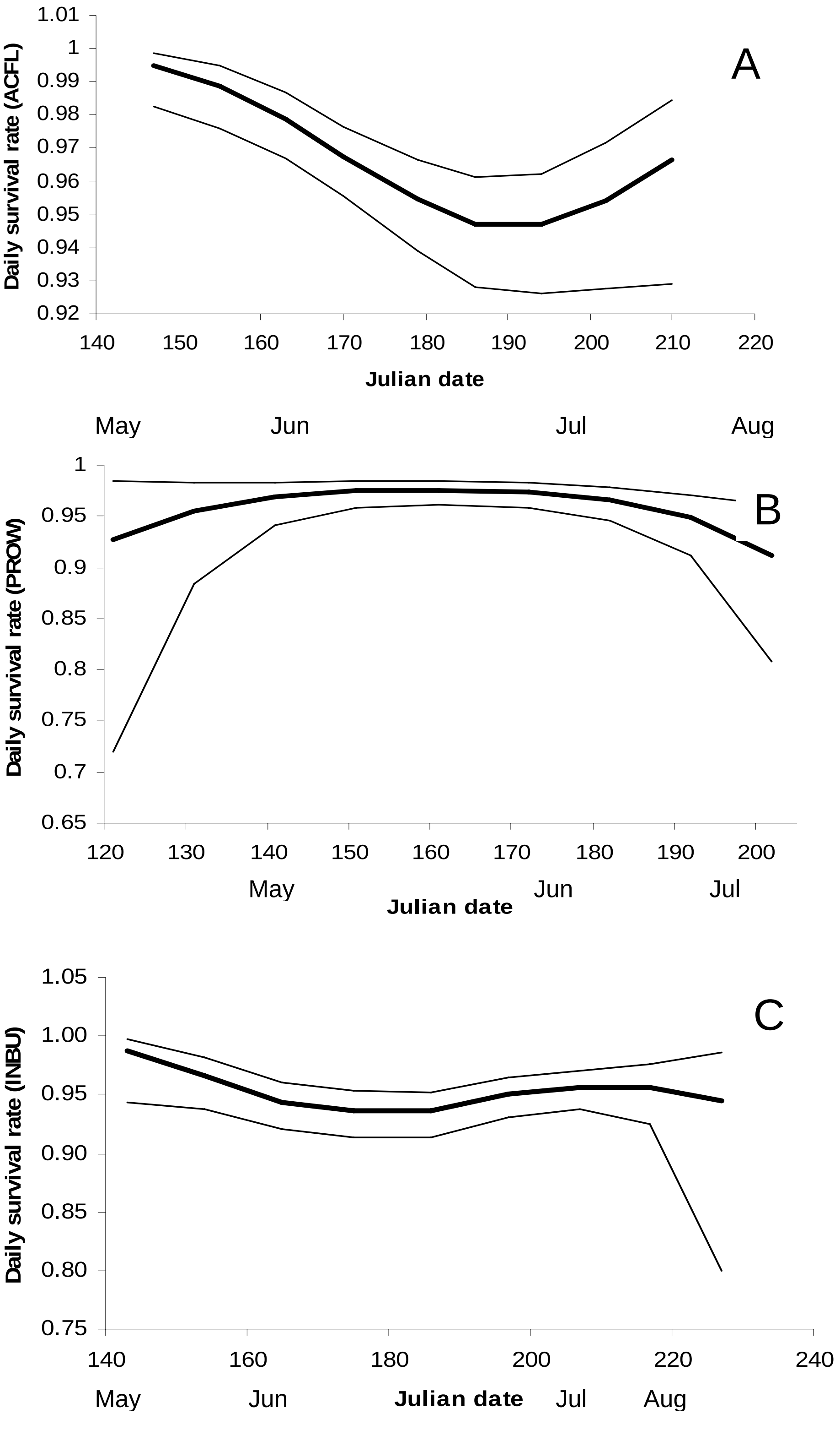

A
Daily survival rate (ACFL)
1.01
1
0.99
0.98
0.97
0.96
0.95
0.94
0.93
0.92
140
150
160
170
180
190
200
210
220
Julian date
May
Jun
Jul
Aug
B
Daily survival rate (PROW)
1
0.95
0.9
0.85
0.8
0.75
0.7
0.65
120
130
140
150
160
170
180
190
200
May
Jun
Jul
Julian date
C
Daily survival rate (INBU)
1.05
1.00
0.95
0.90
0.85
0.80
0.75
140
160
180
200
220
240
May
Jun
Julian date
Jul
Aug

Figure 1-2. Effects of percent forest cover, forest type, and distance to edge on nest survival of focal bird species and 95% CI. (A) Acadian Flycatcher (ACFL) period survival rate (PSR) by percent forest cover in the landscape. (B) Prothonotary Warbler PSR by forest type. (C) Indigo Bunting (INBU) PSR by distance (m) to forest edge.

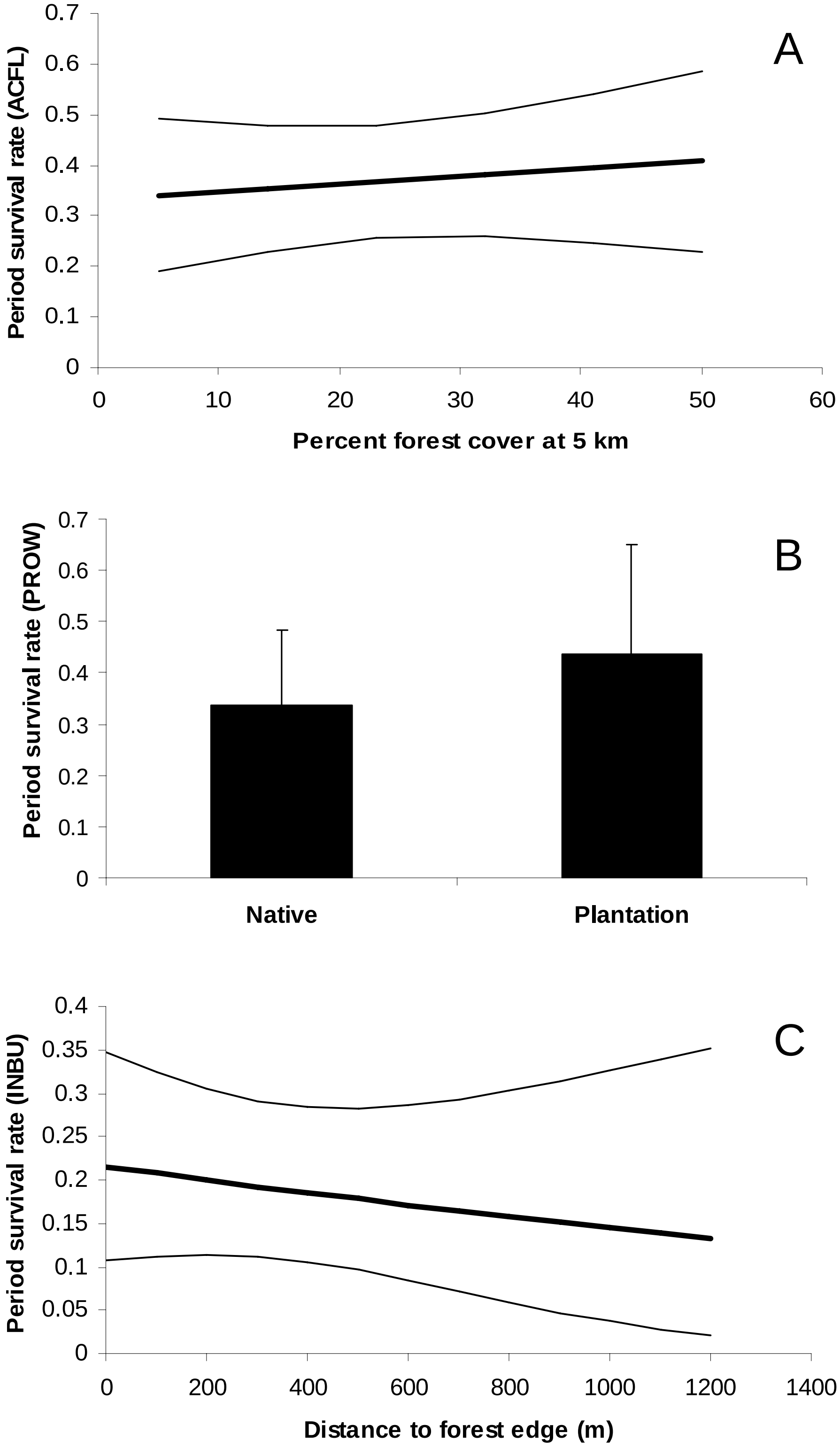

A
Period survival rate (ACFL)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
0
10
20
30
40
50
60
Percent forest cover at 5 km
B
Period survival rate (PROW)
0
0.1
0.2
0.3
0.4
0.5
0.6
0.7
Native
Plantation
C
Period survival rate (INBU)
0
0.05
0.1
0.15
0.2
0.25
0.3
0.35
0.4
0
200
400
600
800
1000
1200
1400
Distance to forest edge (m)

Table 1-4. Model-averaged parameter estimates from the most supported models predicting nest success of Acadian Flycatchers, Prothonotary Warblers, and Indigo Buntings in the Mississippi Alluvial Valley

Variables	Model estimate	# of models	Uncond. SE	Odds ratio	Odds ratio lower 95% CI	Odds ratio upper 95% CI
Acadian Flycatcher						
distwater	0.0000	18	0.0000	1.0000	1.0000	1.0001
intercept	48.8071	18	15.9960	1.57E+21	20078784	1.23E+35
cbpara - n	0.0146	18	0.0694	1.0147	0.8800	1.1658
cbpara - y	0.0000	18	0.0000	1.0000	1.0000	1.0000
cover5	0.0044	18	0.0074	1.0044	0.9900	1.0193
julian	-0.4831	18	0.1757	0.6169	0.4300	0.8765
julian2	0.0013	18	0.0005	1.0013	1.0000	1.0022
Prothonotary Warbler						
julian	0.2471	17	0.1215	1.2803	1.0042	1.6324
julian2	-0.0008	17	0.0004	0.9992	0.9985	0.9999
native	-0.5771	17	0.6218	0.5615	0.1619	1.9476
plant	0.0000	17	0.0000	1.0000	1.0000	1.0000
Indigo Bunting						
distedge	-0.0002	16	0.0003	0.9998	0.9991	1.0005
distwater	0.0000	16	0.0000	1.0000	1.0000	1.0001
height	0.0481	16	0.0813	1.0493	0.8919	1.2345
intercept	142.363	16	84.2684	6.71E+61	0.0000	1.05E+135
2004	0.5520	16	0.2800	1.7368	0.9922	3.0403
2005	0.2922	16	0.2335	1.3393	0.8396	2.1366
2006	0.0000	16	0.0000	1.0000	1.0000	1.0000
cbpara - y	-0.0445	16	0.0950	0.9565	0.7909	1.1568
cover5	0.0027	16	0.0049	1.0027	0.9929	1.0126
julian	-2.2081	16	1.3805	0.1099	0.0070	1.7383

julian2	0.0115	16	0.0075	1.0116	0.9965	1.0269
julian3	0.0000	16	0.0000	1.0000	1.0000	1.0000
patch	0.0001	16	0.0001	1.0001	0.9998	1.0004
nativ	-0.1150	16	0.1915	0.8914	0.6077	1.3074
plant	0.0000	16	0.0000	1.0000	1.0000	1.0000

boxes, not natural cavities. Twenty-three Prothonotary nests were parasitized by Brown-headed Cowbirds.

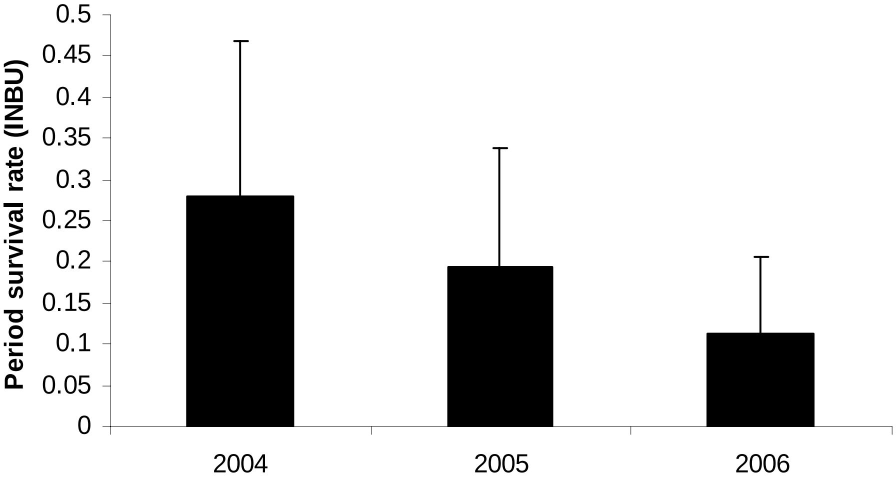
There was substantial model selection uncertainty for both the temporal models and habitat models. The overdispersion parameter of the global model (1.1376) failed to indicate a substantial lack of fit. The most supported temporal model was the Julian^2 model ($w_i = 0.267$). The most supported habitat model included forest type ($w_i = 0.540$; Table 1-2). The second best model included percent native forest cover, percent plantation forest cover and distance to water ($\Delta AIC_c = 3.191$; $w_i = 0.109$). Support for this model would suggest that not only the amount, but the type of forest in the landscape is important to Prothonotary nest survival. The $\Delta AIC_c > 2.0$ and evidence ratio of only 0.20 suggests little support for the second model relative to the best model. However, the landscape model incorporating the percent forest cover in the landscape (regardless of type) was the fifth ranked model with $w_i = 0.047$ and $\Delta AIC_c = 4.884$, indicating substantially less support for pooling forest types. The model averaged daily survival rate (DSR) was 0.976 (0.962 – 0.985) resulting in overall period survival of 0.493 (0.324 – 0.643). Daily survival was 0.93 early in the season, increased to a high of over 0.98 in early June, and then fell to 0.91 at the end of the season (Figure 1-1B). The odds ratio and survival estimates indicated greater survival in plantations, however, confidence limits broadly overlapped (Table 1-3, Figure 1-2B).

Indigo Bunting. We found 205 Indigo Bunting (hereafter bunting) nests comprising 733 intervals. One hundred and eighteen nests occurred in plantation forest and 77 in native forest. Ninety-eight bunting nests were depredated (50.5%). Three depredations occurred during laying, 42 during incubation, and 53 during the nestling stage. In plantation forests, 54 of 117 nests (46.2%) were depredated, while in native forests, 48 of 77 nests (62.3%) were depredated. Sixty-nine nests fledged at least one chick. Eighty-six bunting nests were parasitized by Brown-headed Cowbirds.

The overdispersion parameter of the global model (1.0104) did not indicate evidence for a lack of fit. Considerable model selection uncertainty existed in both the temporal and habitat aspects of the analysis. The top temporal model was the Julian^3+ Year model (w_i = 0.186). The most supported model in the habitat analysis was the null, or temporal model (w_i = 0.157) (Table 1-2). However, seven other models incorporating nest, patch, and landscape effects had $\Delta AIC_c < 2$ (Table 1-2) and should not be ruled out. Nest site variables occurred in four of these six, and patch variables occurred in the second and third selected models. The global model was the poorest performer.

Due to model selection uncertainty and model averaging no effects received overwhelming support from the data (Burnham and Anderson 2002). Model averaged survival rates and odds ratios indicated several temporal and habitat parameters appear to influence daily survival (Table 1-3). Among these, none had odds ratio confidence limits that did not overlap one. However, nests had 73% greater odds of surviving in 2004 than 2006, and 34% greater odds of surviving in 2005 than 2006 (Figure 1-3). Bunting nests in native forest had 11% lower survival odds than those in plantation forests. Indigo Bunting nests near edges had slightly higher period survival rates than those further from an edge (Figure 1-2C). The model averaged DSR for buntings was 0.936 (0.916 – 0.951), resulting in a period survival estimate of 0.191 (0.112 – 0.286). Daily survival ranged from a high of 0.988 in late May to a low of 0.935 in late June, increased in July to 0.957, then decreased the remainder of the season (Figure 1-1C).

Figure 1-3. Indigo Bunting period survival rate by year.



Period survival rate (INBU)
0.5
0.45
0.4
0.35
0.3
0.25
0.2
0.15
0.1
0.05
0
2004
2005
2006

PARASITISM

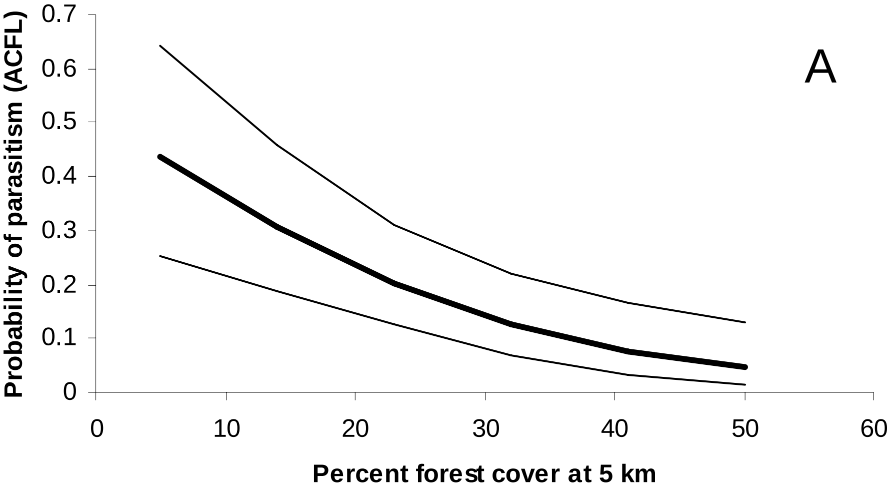
Acadian Flycatcher. Thirty-four of 150 (23%) Acadian Flycatcher nests were parasitized by cowbirds; 28 of 98 (28.6%) in native forest, and six of 52 (11.5%) in plantation forests. The most supported temporal model for cowbird parasitism was the Julian^2 model (w_i = 0.339). The most supported habitat models included percent forest cover plus distance to water or forest patch size or all three of these (Table 1-4). The probability of being parasitized varied between 0.168 (0.099 – 0.269) and 0.280 (0.118 – 0.530) between 27 May and 29 July. There was a negative effect (-0.0347) of forest cover within five km of a nest on the probability of parasitism as percent forest cover increased (Fig 1-4A). However, when model averaged, ninety-five percent confidence limits overlap zero (-0.1093 – 0.0399). The odds ratio likewise indicated a negative effect of forest cover on probability of parasitism, and confidence limits overlapped one.

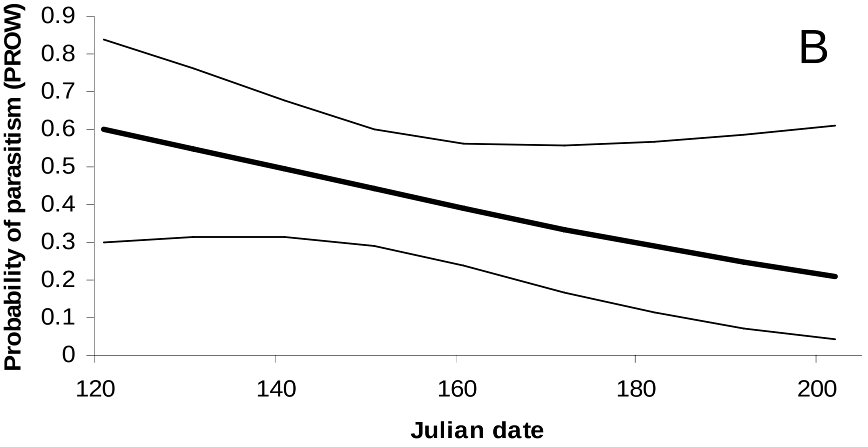
Prothonotary Warbler. Twenty-five of 75 (33%) Prothonotary Warbler nests were parasitized by cowbirds; 22 of 49 (44.9%) in native forests and three of 26 (11.5%) in plantation forests. Two of the parasitism events in plantation forest were in artificial nest boxes. For all natural cavity nests regardless of forest type, 23 of 52 (44.2%) were parasitized.

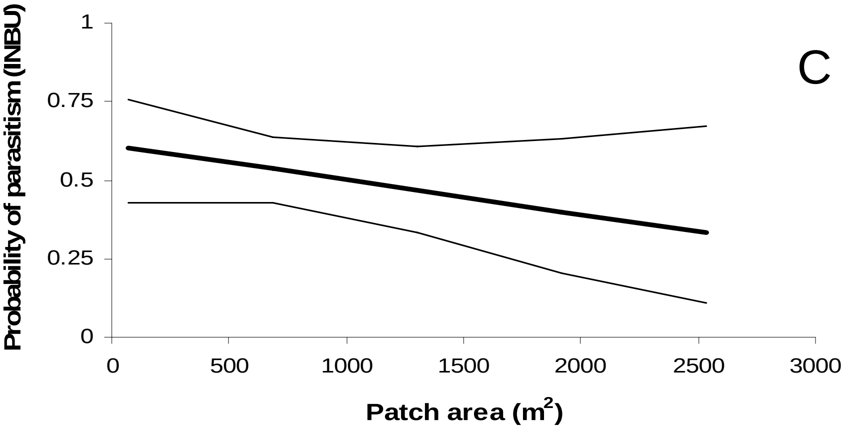
Table 1-5. Support for the most supported candidate models (∆AICc < 2.0.) used to evaluate factors affecting brown-headed cowbird parasitism of Acadian Flycatcher, Prothonotary Warbler, and Indigo Bunting nests in the Mississippi Alluvial Valley.

Model	logL	K	ΔAIC_c	w_i
Acadian Flycatcher				
julian + julian^2 + cover5 + distwater	-71.117	5	0.000	0.304
julian + julian^2 + patch	-70.557	6	1.049	0.180
julian + julian^2 + cover5 + distwater + patch	-70.856	6	1.649	0.133
Prothonotary Warbler				
julian	-34.657	3	0.000	0.337
julian + distwater	-34.250	4	1.537	0.156
julian + cover5	-34.265	4	1.567	0.154
Indigo Bunting				
julian + julian^2 + patch	-118.701	7	0.000	0.237
julian + julian^2 + patch + height	-117.743	8	0.268	0.208
julian + julian^2 + patch + cover5 + distwater	-118.521	8	1.823	0.095

Figure 1-4. Probability of parasitism and 95% CI by Brown-headed Cowbirds. (A) Probability of parasitism of Acadian Flycatchers (ACFL) with varying percent forest cover at 5 km from nest. Panel does not include model averaging. (B) Probability of parasitism of Prothonotary Warbler (PROW) by Julian date. (C) Probability of parasitism of Indigo Buntings (INBU) with varying forest patch size (m^2).


A
Probability of parasitism (ACFL)
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
10
20
30
40
50
60
Percent forest cover at 5 km


B
Probability of parasitism (PROW)
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
120
140
160
180
200
Julian date


C
Probability of parasitism (INBU)
1
0.75
0.5
0.25
0
0
500
1000
1500
2000
2500
3000
Patch area (m^2)

The most supported temporal model included only the Julian date variable (w_i = 0.411). There was limited support for any habitat effects on the probability of parasitism. The best supported habitat model was the null (temporal) model (w_i = 0.337; Table 1-4). The second most supported model included distance to water (w_i = 0.156), and the third model included percent forest cover within 5 km of the nest (w_i = 0.154; Table 1-4). The probability of parasitism declined through the breeding season (Figure 1-4B), but this and the other effects in the top models had odds ratio confidence intervals that overlapped 1.

Indigo Buntings. Eighty-six of 195 (44%) bunting nests were parasitized by cowbirds, 41 of 77 (53.2%) in native forests and 45 of 118 (38.1%) in plantation forest. The best temporal model was the Julian^2 model (w_i = 0.448). The best habitat model included forest patch size (w_i = 0.237) and forest patch size was in all the top models (Table 1-4). The second best model also included nest height and the third most supported model included percent forest cover and distance to water (Table 1-4). Probability of parasitism increased from 0.39 (95% CI: 0.18, 0.66) at the beginning of the breeding season to 0.54 (95% CI: 0.44, 0.64) in late June and early July and then decline to the end of the season in early August. Odds ratios indicated a negative effect of patch area on parasitism in the top two models but when model averaged the confidence interval overlapped 1. However, predicted probability of parasitism ranged from 61% in the smallest patches (68 hectares) to 34% in patches of 2500 ha (Fig. 4-4C).

Discussion

NEST SURVIVAL

Our primary interest was whether breeding habitat quality of plantation forests was substantially less than native fragments. Neither open-cup nesting species showed a significant influence of forest type on nest survival, suggesting that at least some open-cup nesting birds in this landscape experience similar pressures in both forest types. Therefore, plantation forests may be useful conservation tools for providing additional nesting habitat to migratory birds. Hazler et al. (2006) found similar results for Acadian Flycatchers in South Carolina pine (*Pinus* sp.) plantations, indicating that this species may be more behaviorally flexible than previous information would suggest (Whitehead and Taylor 2002).

Our findings contrast those in Louisiana, where open-cup nesters had higher DSR in native forests (0.951 ± 0.002) than in cottonwood plantations (0.929 ± 0.003) (Twedt et al. 2001). Twedt et al. (2001) attributed this to higher rates of predation and parasitism in plantations, however, they combined open-cup nests of multiple species due to small sample size, and acknowledge that this may mask important, species-specific conclusions. For example, we found slightly lower rates of parasitism on nests of Acadian Flycatchers in plantations, which may result from the uniformity of the habitat and resultant lack of perches from which female cowbirds can nest search (Chace et al.

2005). In addition to nest site characteristics, there may have been latitudinal differences between our study plots and those in Louisiana (Thompson 2007). For example, fire ants (*Solenopsis wagneri*) were not observed on our sites, but were important nest predators in plantations further south (Twedt et al. 2001).

Cavity nesting Prothonotary Warblers had substantially different results from the open-cup nesters. Nest survival was slightly higher in plantation forests although confidence intervals overlapped substantially due to model averaging. All but three nests in plantation forests occurred in artificial nest boxes, potentially confounding the results. However, nest success of Prothonotary Warblers is similar in boxes and natural cavities in Illinois (Hoover 2006b). Differences in cavity nest survival between the habitat types may occur, but the potential for increased nest survival associated with nest boxes can not be ruled out in this case (Møller 1989; Kuitunen and Aleknonis 1992). Given the range of published nest survival rates across species, our findings suggest that cottonwood plantations can provide breeding habitat comparable to native forests for at least some species (Robinson et al. 1995; Twedt et al. 2001; Gram et al. 2003).

Some studies have found a link between landscape-level forest cover, fragmentation levels, and nest survival (Robinson et al. 1995), while others have found no support for higher levels of forest cover improving productivity (Burke and Nol 2000). Although we found limited support for models incorporating percent forest cover at the 5 km scale, Acadian Flycatcher nests exhibited a notable positive trend with increasing forest cover (Figure 1-2A). Percent forest cover by type within a 5 km radius circle was the second best model for Prothonotary Warblers. Increases in survival as seen in Acadian Flycatchers, may be biologically meaningful. Our results suggest that even small increases in forest cover in this landscape would positively influence nest survival for some species. Increasing individual patch sizes, and contiguity of existing forest cover would achieve this goal and likely improve habitat quality for a variety of species.

Indigo Bunting exhibited a negative correlation between nest survival and distance from an edge (Figure 1-2C). Given the small size of most of the forest patches on our site, most areas are potentially saturated with nest predators (Chalfoun et al. 2002b). We regularly observed several species of snakes and small mammals (raccoons and opossums) on our study plots, as well as known avian nest predators, such as Red-bellied Woodpeckers and Red-shouldered Hawk. We suggest lower survival away from edges occurs because buntings nest low to the ground and higher stem density and shrub cover near edges provides greater concealment for nests. Edges of native forest were a consistently dense and difficult barrier, and although plantation understory tended to be more uniformly dense throughout, edges were typically more densely vegetated in plantations as well.

While nest survival is similar between habitats, the overall quality of both habitats for breeding is questionable. Donovan and Thompson (2001) suggested for a generic neotropical migrant bird with adult survival of 0.6, juvenile survival of 0.3, and two female fledglings per successful nest and that made up to 3 nest attempts requires a nest survival of 0.3 to maintain a stable population. My nest survival estimates for Acadian Flycatcher and Prothonotary Warbler exceeded this but were much less for Indigo Buntings. Furthermore, my observations of number of fledglings per successful nest was low (Acadian Flycatcher 2.27, Prothonotary Warbler 3.13, Indigo Bunting 2.56), likely as a result of parasitism. Assuming a 50:50 sex ration this lower fledging rate would require nest survival of greater than 0.5 for a stable population (Donovan and Thompson 2001). Unless other compensating factors offset low fledgling rates and observed nest success (i.e. higher individual survival or more nest attempts) these local populations may not be self sustaining. This is especially true for Indigo Buntings, however, this contrasts strongly with the observation of very high densities of buntings in this landscape (M. Shane Pruett, pers. obs.). This suggests Indigo Buntings are immigrating from other areas or that birds breeding in alternative habitats not included in this study (i.e. field borders, strip cover along ditches, or other non-forest habitat) are more productive and sustaining the local population. Further study will be needed to determine whether this is the case and if so, how nest survival compares in these habitats with forest nesting populations.

Our findings paint a complex picture of avian nest survival in a heavily altered landscape. Survival seems comparable between forest types, and if this remains the case in areas with a greater percentage of forest cover on the landscape, we expect plantations to represent a useful alternate habitat for some forest nesting migrant passerines. Unfortunately, habitat variables that we measured provided little information for explaining nest survival in this landscape, characterized by extreme levels of fragmentation and the abundance of cowbirds and predators. Other, unmeasured variables such as food availability and quality may influence temporal variation that we observed, as well as overall nest productivity and therefore represents an opportunity for further research (Zanette et al. 2006). For example, Bakermans and Rodewald (2006) found that successful Acadian Flycatcher territories had 60% greater understory arthropod biomass than territories with unsuccessful nests. If highly fragmented or agricultural landscapes alter food quantity or quality or negatively influence other necessary resources, birds nesting in such environments may have a difficult time adequately provisioning young.

NEST PARASITISM

Models incorporating percent forest cover at 5 km (Acadian Flycatcher) and patch area (Indigo Bunting) best explained the probability of parasitism for the open-cup nesting species. Our findings are in accord with other findings in the Midwest, where severe fragmentation has been linked to lower nest survival and higher parasitism. There was considerably more uncertainty regarding the best model for parasitism of Prothonotary Warbler nests in our analyses. Low sample size and small diameter of holes provided in plantation nest boxes probably account for the lack of a standout model for this species. Smaller holes likely decrease the probability of parasitism. The holes in our nest boxes were 31.75 mm in diameter. Hoover (2003) found that in southern Illinois boxes with 32 mm holes were never parasitized, while all boxes with 44 mm and 54 mm holes were parasitized. His sample size for the small holed nests was very small, and this could account for the discrepancy of our results. Additionally, if host nests are limiting in plantations, and cowbirds are forced to lay eggs in any available nest, the small holes in our boxes may not act as a deterrent.

The substantial reduction in likelihood of parasitism with increasing forest cover for Acadians supports our belief that increases in forest cover in this region would be highly beneficial to forest nesting species. Although there was not support for an effect of forest cover on parasitism of indigo buntings, parasitism did decrease with increasing patch size. We suggest efforts to increase forest cover should focus on enlarging existing forest patches and enhancing connectivity, thereby increasing core areas for forest breeding birds. Additionally, although mature, native forest structure and composition are important for the maintenance of some songbird populations (e.g. Cerulean Warbler (*Dendroica cerulea*), Swainson's Warbler (*Limnothlypis swainsonii*), secondary cavity nesters), our finding that parasitism rates were generally lower in plantations suggests that these forests may provide a viable, alternative breeding habitat for at least some species if daily survival rates were not so low that the habitat likely functions as a sink.

Parasitism of Prothonotary Warbler nests declined consistently throughout the breeding season. Prothonotary Warblers start breeding earlier than our other study species, and it is possible that as more open-cup nests become available, Prothonotary Warblers are less targeted for parasitism. Increasing levels of parasitism on Indigo Buntings in the late spring and early summer may indicate cowbirds switching to this common species as the landscape becomes saturated with their nests. The slight increase in parasitism rates for Acadian Flycatchers at the end of the summer was surprising, and may indicate that when alternate nests become less common as early breeding species terminate nesting, cowbirds are forced to parasitize more Acadian nests, even though cowbird success when parasitizing this species may be lower than for other hosts (Ford et al. 2001).

The low to moderate nest survival estimates for our focal species and the high parasitism levels, though not necessarily causative are related in important ways. For example, our findings that Acadian Flycatcher nest survival increases and parasitism decreases as forest cover increases suggests that parasitism may exacerbate other problems even when it is not the strongest influence. This underscores potential benefits to be gained by increasing forest cover in the landscape. The decline of parasitism rates with increasing patch size for indigo bunting further supports the need for increased forest cover as a mitigating factor for nesting birds in this system. Our nest survival estimates include nests successful, but producing only cowbird fledglings, and therefore represent a best possible scenario. Production of host nestlings is therefore lower than suggested by nest survival rates alone. Increases in forest cover would likely reduce parasitism pressures on birds nesting in fragmented bottomlands. As a result, losses directly attributable to parasitism should decline, and nest survival more accurately reflect reproductive success of forest nesting birds.

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Chapter 2 – Comparing Avian Density Estimation Methods from Point Count Data in Two Forest Types

Introduction

Environmental features and characteristics intrinsic to individual species influence avian breeding density either by direct effects on spacing or through the interaction between external and internal factors (Newton 1998). Habitat-specific effects include the availability of suitable nest sites (Twedt and Henne-Kerr 2001), patch size or shape (Peak and Thompson 2006), and species composition, both in native (Sallabanks et al. 2000) and altered (Remeš 2003) habitats. Land managers often exert tremendous control over these habitat attributes through their land use decisions. The Mississippi Alluvial Valley (MAV) has been drastically altered since colonial times by ditching, deforestation, and levee construction (Fredrickson 2005, King et al. 2005). Conversion to agriculture has had the most dramatic influence on community structure and function (Schoenholtz et al. 2005). Flooding of cropland during the 1990's renewed interest in hardwood forestry (i.e. pulpwood production) in the flood prone low-lying areas (Twedt and Uihlein 2005). During the same period, the MAV Migratory Bird Planning Group was formed and initiated efforts to coordinate the management of migratory bird conservation along the Mississippi river corridor. One of the primary recommendations was hardwood reforestation of significant portions of the region (Brown et al. 1999, Mueller et al. 1999). Research in experimentally managed forests in Louisiana indicated successful utilization by migrant songbirds of fast growing species such as cottonwood (*Populus deltoides*)

(Twedt et al. 1999, 2001). Twedt et al. (1999) found that cottonwood plantations enhanced breeding bird populations over agricultural areas. However, they found the breeding assemblages to differ between cottonwood plantations and mature bottomland hardwood (BLH) forest. Differences in the value of the habitats were therefore obscured by potential differences between the species inhabiting each forest type. Based on an indicator value of the species using each habitat and a Partners In Flight (PIF) prioritization score, bottomland forests ranked twice as valuable as regenerating cottonwood stands for avian conservation (Twedt et al. 1999). No such assessment has occurred in the upper MAV which is more highly drained and fragmented than many lower lying areas to the south. Further, no study in the region has directly compared breeding densities of the same species in the two habitat types.

Current forest cover in the Missouri portion of the MAV is about 6% of the original largely contiguous, forest, and 98% of the patches are < 1012 ha (Twedt and Loesch 1999). However, remnant native forests and plantations host a surprising array of breeding migrant songbirds. At least 87 species were recorded during the summer breeding season in southeast Missouri floodplain forests (Papon 2002). Numerous Partners in Flight (PIF) species of continental importance (Rich et al. 2004) occur in both native and plantation forests. Small populations of watch list species such as Cerulean warbler (*Dendroica cerulea*), Swainson's warbler (*Limnothlypis swainsonii*), and Kentucky warbler (*Oporornis formosus*) breed in the native forests. PIF stewardship species such as Acadian Flycatcher (*Empidonax virescens*), Carolina wren (*Thryothorus ludovicianus*), Prothonotary Warbler (*Protonotaria citrea*), and Indigo Bunting (*Passerina cyanea*) are found regularly breeding in both forests (Papon 2002). Based on

Breeding Bird Survey data (http://www.mbr-pwrc.usgs.gov/bbs/), none of these species appear to be declining significantly in this region; however, many of the trends were generated on very scant sample sizes and are based on unadjusted count data.

Although no significant effects of fragmentation on nest survival were found in native forests or plantations in the region, larger patch size and higher percentages of forest in the landscape appeared to positively influence nest survival (Pruett 2008). Period survival rates are similar in plantation and native forests, suggesting productivity may be similar in the two habitats (Pruett 2008). However, we suspected that abundance would differ between the two forest types, presumably due to structural differences. If so, inferences based solely on nest survival rates would lead to erroneous conclusions about the potential productivity of the two forest types.

Breeding abundance directly influences the relative productivity of different habitats. While abundance measures alone may be insufficient for assessing relative habitat quality (Van Horne 1983, Vickery et al. 1992, but see Bock and Jones 2004), in combination with other demographic parameters, they can provide important insights into the relative quality of different habitats and how they influence population demography (Pidgeon et al. 2003). Field researchers therefore need suitable methods for estimating abundance. Comparing results from various studies may be informative, but differences in geographic location, landscape influence (e.g. forests in agricultural versus suburban settings), and habitat type, as well as temporal variation make accurate, direct comparison of results difficult at best. All of these factors, in addition to variation between individuals and over time (e.g. early vs. late morning) create differential detectability among individuals within a population (Seber 1973, Nichols et al. 2000). Methods that do not account for these differences have been strongly discouraged because they fail to adjust count data appropriately for varying detection probability (Rosenstock 2002). Uncorrected counts implicitly assume that count tallies accurately reflect actual population similarities or differences. Traditional methods using uncorrected count data to generate abundance indices fail to estimate detectability, and therefore may be biased.

Abundance estimation has received considerable attention in recent years, particularly in relation to the analysis of avian point count data (Nichols et al. 2006). Specifically, research has focused on methodological improvements for gathering point count data such that accurate and useful information can be extracted (Nichols et al. 2000, Farnsworth et al. 2005). Much recent work has focused on estimating detection probability by effectively modeling the information available in count data (Nichols et al. 2000, Farnsworth et al. 2002, Diefenbach et al. 2007). Methods under current consideration involve double-observer counts (Nichols et al. 2000), distance sampling (Buckland 2006), and removal or recapture models (Farnsworth et al. 2002, Alldredge et al. 2007a). Double-observer methods utilize the individual detections by each counter to estimate observer-specific detection probability (Nichols et al. 2000). Distance sampling builds detection probabilities as a curve fitted to the data, describing how the probability of detection declines with distance away from the point (Buckland 2006). Removal and recapture models subdivide the sampling period into multiple intervals. Removal methods model detection based on a decline in the number of individuals removed (detected) over consecutive intervals (Farnsworth et al. 2002) and recapture models use the encounter history of each individual to model overall probabilities of detection for the population (Amstrup et al. 2005).

An additional advantage to modeling detection is the ability to evaluate hypotheses about various factors that can influence the detectability of individual birds (Marques et al. 2007). Individuals can differ in their detectability due to behavior, location, environmental factors, and differences between observers (Rosenstock et al. 2002). In addition to heterogeneity due to these factors, previously detected individuals may have higher or lower probability of detection in subsequent intervals (a behavior response; Otis et al. 1978). Probability of detection decreases with distance (Buckland et al. 2001), may differ by habitat type (reflecting differences in vegetative structure; Nichols et al. 2000), and may reflect temporal variation within or among counts (Alldredge et al. 2007a). The ability to model heterogeneity effectively, even when the specific source of heterogeneity may remain unknown, reduces the potential for bias inherent in unadjusted count data, and thus raises the legitimacy of comparisons between different habitats.

Our first objective was to compare abundance between native and plantation forests and estimate habitat specific breeding densities. Although numerous recent authors have argued that any method used for such a comparison must incorporate estimates of detection probability, there is no consensus regarding which method or methods are most useful and efficient. Our second objective was therefore to compare methods for estimating abundance, including uncorrected counts (relative abundance indices), capture-recapture, removal, and distance sampling in the same geographic location and in two habitat types (pulpwood plantation forests vs. native BLH forests) and utilizing the same data set. Last, within the context of modeling abundance via the methods above, we evaluated factors potentially affecting individual detectability. We developed hypotheses regarding the effects of several innate characteristics and spatiotemporal factors we believed would influence the detection process. We also incorporated temporal variables accounting for differences between years, for declining detectability as the breeding season progresses, and as activity falls throughout the day.

Study Sites

Our study was conducted in the New Madrid floodplain in BLH and plantation forests of the southeastern Missouri portion of the Mississippi Alluvial Valley (Mississippi and New Madrid Counties) and on two Kentucky islands in Carlisle and Hickman counties. Our study plots included Donaldson Point and Ten Mile Pond Conservation Areas (Missouri Department of Conservation) and Big Oak Tree State Park (Missouri Department of Natural Resources). The remainder of our study sites were in private ownership. Study plots were initially selected in the context of a larger faunal study (Papon 2002). Sixteen four mi^2 blocks were randomly selected from over 250 possible blocks in the Missouri MAV. The sizes of the forest patches are varied and depend on pre-existing forest conditions, whether natural or planted (Table 2-1). The study area is bounded to the east by the Mississippi river. Row cropping of soybeans, corn, millet, and sunflowers is the predominate land use. Most of this landscape is subject to periodic flooding, which historically resulted in a highly diverse vegetative community structured by the microtopography of the floodplain (Conner and Sharitz 2005).

Remnant BLH forests on the study sites are characterized by a mix of deciduous tree species including oaks (*Quercus* spp.), willows (*Salix* spp.), hickories (*Carya* spp.), ash (*Fraxinus* spp.), maples (*Acer* spp.), sugarberry (*Celtis laevigata*), and American sycamore (*Platanus occidentalis*). The forest, excepting a small section of Big Oak Tree State Park, is in various stages of secondary growth and development, but all areas have achieved mature forest structure, with a generally closed canopy, multi-layered subcanopy, and variable ground-level vegetation consistent with heterogeneous inundation of the forest floor. Cottonwood is the most commonly planted tree in plantations (M. S. Pruett pers. obs). Stand structure is determined largely be time-since-planting. Younger stands progress from dense, scrub-shrub-like structure into an intermediate "young-forest" stage with a low, closed canopy and open understory, and finally into a more mature stature, with larger trees, intermediate canopy closure, and a dense herbaceous and vine-rich understory. We utilized plantation forests four to eight years post planting, when young forest stature had been achieved and the bird community shifted from mostly shrub-scrub species to forest species.

Table 2-1. Locations, forest type, patch size and percent forest cover for avian point counts in southeast Missouri, 2006-2007. N = native forest, P = plantation. Patch size is presented in hectares. Percent forest cover within a 5 km radius around the count site.

Site	Forest type	Patch size	% Forest – 5km
Big Oak	N	412.70	16.99
Corse	N	89.54	6.25
Donaldson	N	2531.67	39.45
Gertrude	N	81.28	8.90
Island 3	P	413.30	30.98
Medlin	N	68.17	14.40
Ten Mile	N	731.52	13.50
Winchester	P	721.10	45.75
Wolf	P	1457.43	30.85

Methods

Point Counts

We conducted point counts in native bottomland forest fragments and cottonwood plantations in late May and early June, 2006 and 2007.. Counts were conducted between 0545 and 0900 hours, central daylight time and discontinued anytime wind or precipitation impeded detection or bird activity. We walked parallel transects in native forests and plantation forests from 4 to 8 years old. The starting point for a transect was randomly selected. Points were at least 100m from a hard edge, and all points were at least 200m apart. All surveys were conducted by S. Pruett.

To reduce the potential for double counting individual birds we limited our count to three common PIF species of continental importance (Rich et al. 2004): Acadian Flycatcher (*Empidonax virescens*), prothonotary warbler (*Protonotaria citrea*), and indigo bunting (*Passerina cyanea*). All three species are found nesting regularly in native BLH forest with appropriate structure. Acadian Flycatchers seem to prefer open understory and semi-open subcanopy. Indigo Buntings nest commonly in canopy gaps, edges, and open understory, and Prothonotary Warblers prefer older forests with large numbers of cavity-containing snags or dead limbs. In plantation forests, indigo buntings are one of the most commonly observed breeders. Acadian Flycatchers prefer plantations where tress have begun shedding subcanopy limbs. They also seem to select nest sites where vines have grown into the trees and provide a different nest substrate structure than found in vine-free trees. Prothonotary Warblers are often found along the margins of plantations, and usually only nest in patches where woodpeckers have produced cavities.

We waited 2 minutes after arrival to start the count for activity related to observer movement to subside (Buckland et al. 2001). We counted all males heard or seen during a five minute count period, recording the approximate location of each individual, as well as whether or not it was detected during each one minute interval. Throughout this manuscript, the terms detection, sighting, and capture are used interchangeably to denote an observation of a bird.

All bird locations were estimated and marked on a point map during the count, and notations indicated bird movements during the point. At the close of the count period, the distance to each bird was estimated as accurately as possible, i.e. the snapshot method described by Buckland et al. (2001). For visually detected birds or singing birds for which an exact location was known, distances were generated using a laser range-finder (Bushnell Yardage Pro Compact 800). For birds at greater distances we walked as far as necessary towards the bird's current, or best estimated position and measured the distance from the original point. Some birds were not located exactly due to movement away from their original position, or to inactivity during the distance measurement. These locations were estimated as close as possible to the original detection site. Based on regular observer self-testing, at the time of counting we believed the majority of these estimates to be accurate to around ± 10m.

Data Analysis and Parameter Estimation

We compared abundance estimates generated from unadjusted counts, distance sampling, removal models, and capture-recapture (recapture) models. To standardize our sample area for comparison purposes and to eliminate outliers (Alldredge et al. 2007a), we truncated the data by removing observations composing the top 10% of detection distances (Buckland et al. 2001) for model-based methods, but not for the traditional count method. We felt justified in this comparison because one of the largest and longest running point count protocols, the Breeding Bird Survey, uses a 0.25 mile (400 m) radius count circle (http://www.pwrc.usgs.gov/BBS/). For forest nesting passerine birds this essentially represents an unlimited radius count. Results for model-based methods are converted to mean number of detections per point for direct comparison with traditional unadjusted (means) estimates, which are often presented as relative abundance indices instead of being converted to densities (Howell et al. 2004). The model-based methods we used lend themselves to density estimation because they estimate probability of detection, from which abundance can be directly calculated. We were unable to objectively determine which method is "best" because true abundances were unknown. Instead we focus on comparing the point estimates, confidence intervals, and inferences obtained from each method.

We reduced the number of models run in each analysis by first running an analysis of model structures without associated covariates, and then carrying the best model from each analysis forward as the null model for comparison with candidate models with additional covariates representing factors hypothesized to affect detection probability. During the first analytical stage, we evaluated support for models incorporating differences by habitat type because we were interested in whether heterogeneity differed by habitat (explained in detail under removal and capture recapture models below).

Distance sampling.— We used program DISTANCE, version 5.0 (Thomas et al. 2005) to generate detection functions based on the declining detectability of birds with distance from the observer (Buckland et al. 2001). We fitted half normal, hazard-rate, and uniform functions with cosine, polynomial, and hermite polynomial expansion terms to the data and used information theory to determine which best fit the data. The best fitting detection function for all species was a uniform function, which does not allow analysis of covariate data. To evaluate support for temporal covariates in the data we therefore brought both the uniform key model and the most supported non-uniform key forward into the second stage of analysis (Table 2-2). This allowed us to compare the best detection function overall (uniform key), with covariate models (either half-normal or hazard rate) to determine whether inclusion of covariate data improved our ability to explain the detection process.

Table 2-2. Most supported detection functions for each species derived from Program Distance. For all species a uniform function key was most supported, therefore most supported non-uniform function also presented to facilitate covariate analysis.

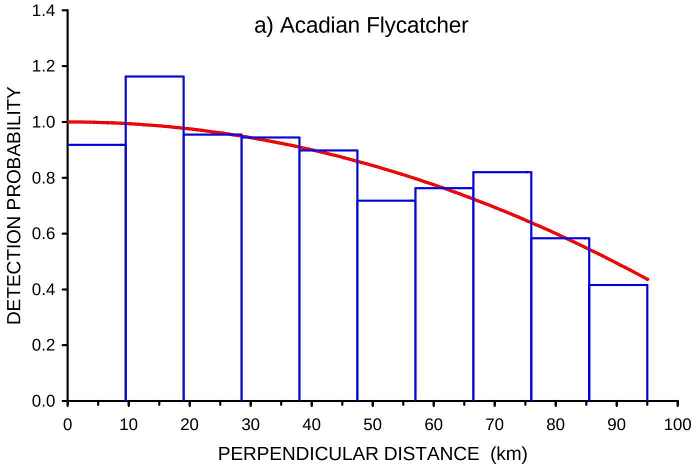
	Key parameter and series expansion		K	AIC_c	ΔAIC_c	w_i
ACFL	Uniform	Simple polynomial	1	3475.707	0	0.275482
	Half-normal		1	3475.919	0.211914	0.247786
PROW	Uniform	Cosine	1	1630.538	0	0.231428
	Hazard rate		2	1630.733	0.195	0.209929
INBU	Uniform	Cosine	1	5799.049	0	0.369276
	Hazard rate		2	5800.441	1.39209	0.184104

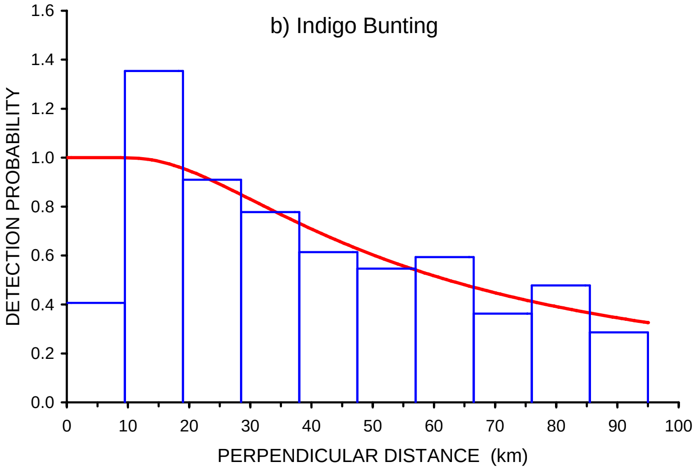
We used multiple covariate distance sampling (MCDS) to model the temporal and habitat variables as additive effects to the best non-uniform model, and used AIC$_c$ values and model fit to determine the most parsimonious model. We assessed the fit of all models visually (Figure 2-1) and by the $\chi 2$ goodness of fit test (Buckland et al. 2001). We then calculated densities for native and plantation forests based on the best covariate model, or uniform model if no covariates improved the fit.

Removal/Capture-recapture.— We analyzed removal and recapture models in program MARK using Huggins closed capture data types, which allow incorporation of individual covariates for each individual detected. We grouped data by the habitat type (e.g. plantation or native forest) in which points were conducted. Each detection included the associated covariate values for the variables Julian date, minutes since sunrise, year, and distance (Table 2-3).

Traditional removal models include only the time of first detection (Farnsworth et al. 2002), while behavior-removal models and recapture models incorporate the entire detection history of each individual (Alldredge et al. 2007a). For example, a bird detected in the first, second, and fourth intervals would have a traditional removal history of 10000 and a behavior-removal and recapture history of 11010, where one represents a detection during an interval and zero represents a failure to detect. Removal methods model detection probability as a function of the decline in captures over sequential sampling periods. Recapture models incorporating a behavioral response likewise model abundance from the decline in new captures over time.

Figure 2-1. Detection functions for most supported distance model used to estimate abundance for each species. a) Acadian Flycatcher –uniform key, no expansion term, no covariates; b) prothonotary warbler – hazard-rate key, cosine expansion, year, and julian date covariates; c) indigo bunting –hazard rate key, cosine expansion, year covariate.


a) Acadian Flycatcher
DETECTION PROBABILITY
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
70
80
90
100
PERPENDICULAR DISTANCE (km)


b) Indigo Bunting
DETECTION PROBABILITY
1.6
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
70
80
90
100
PERPENDICULAR DISTANCE (km)

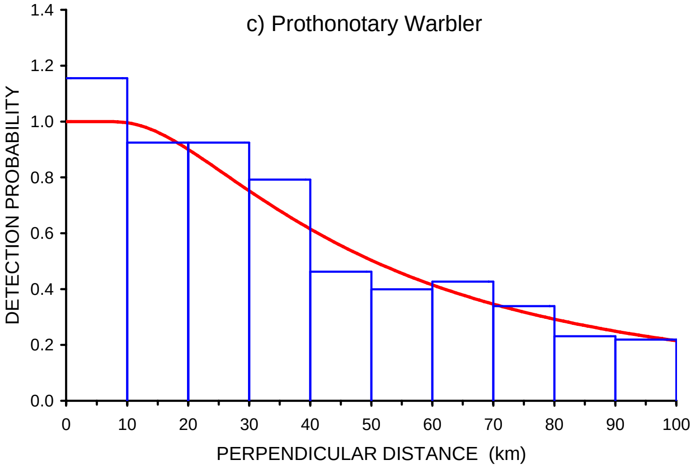

c) Prothonotary Warbler
DETECTION PROBABILITY
1.4
1.2
1.0
0.8
0.6
0.4
0.2
0.0
0
10
20
30
40
50
60
70
80
90
100
PERPENDICULAR DISTANCE (km)

Table 2-3. Basic model structures, covariate effects, and associated hypotheses for removal and capture-recapture models of detection probability. Top model set represents intercept models. For each model shown (with the exception of Mh1) there were two models in the actual set, representing differences by forest type and no difference by forest type (e.g. Mo_Hab and Mo_NoHab). We carried the most supported model forward as the intercept for the second stage of analysis. Bottom set lists additive single covariate models. x subscript denotes an intercept model structure from top set. Full model set for each species includes the best intercept model and all single and multiple-covariate combinations.

Stage 1 Analysis

Model	Variable(s)	Hypothesis
M_o		Probability of detection constant
M_b	behavior	Initial detection probability differs from subsequent detections
M_{h1}	heterogeneity	Population consists of two detectability groups - easy and difficult, but groups similar in both habitats
M_{h2}	heterogeneity by habitat	Population consists of easy and difficult to detect groups, and group composition differs by habitat
M_{bh1}	behavior + heterogeneity	Two detectability groups across habitats; initial detection probability differs from subsequent
M_{bh2}	behavior + heterogeneity by habitat	Two detectability groups but different in each habitat; initial detection probability differs from subsequent

Mx_J	julian date	Probability of detection declines with date
Mx_D	distance	Probability of detection declines with distance from point
Mx_M	minutes since sunrise	Probability of detection declines throughout the morning
Mx_Y	year	Probability of detection differs by year

They also estimate the probability of recapture, but do not utilize the recapture information available in the data for estimating abundance. Recapture models excluding behavior estimate detectability based on the complete detection history of each individual. Because the most supported recapture model always incorporated behavioral response and would therefore estimate abundance as a removal model (Farnsworth et al. 2002), we also carried the best non-behavior model forward to produce recapture model results, because we were specifically interested in how recapture model results compared to removal models. Other than the behavioral response, we did not allow detectability of individuals to vary over the different intervals.

As with the distance analysis, we used a two-stage approach to analyze recapture and removal data sets. We first evaluated support for intercept and intercept + habitat models . Intercept-only models (Table 2-3 – top) included either constant detection probability (M_o) or detection probability varying due to individual heterogeneity (M_h). Recapture models included a parameter for a behavioral response, allowing different probability of recapture, given an initial capture (i.e. a trap-happy response). We believe tracking individuals across the count period to avoid double counting, increases the probability of resighting in subsequent intervals. We also evaluated support for models structure exactly as above, but grouped by habitat type, to determine if habitat was fundamentally important to the detection process.

Individual birds may differ in detectability for a number of observable or unobservable reasons; such unknown heterogeneity can arise from innate differences between individuals (e.g. mated vs. unmated; experienced vs. first-time breeder;

topographic variation) resulting in easy and difficult to detect groups of birds (Farnsworth et al. 2002; Alldredge et al. 2007a). We hypothesized that individual heterogeneity would be an important component of detectability. Individual heterogeneity in point count analysis can be modeled with finite mixture models which allow the population of interest to be composed of a finite number of subgroups, each with its own detection probability. We used a two point mixture, which models birds as either easy or difficult to detect (Pledger 2000, Alldredge et al. 2007a). The models incorporate an additional parameter (*Pi*) describing the probability that a randomly selected individual is a member of the difficult to detect group.

If heterogeneity is due to innate, unmeasured, individual characteristics, we expect support for models including a single estimate of *Pi* across both habitat types. However, if heterogeneity is not simply variation among birds, but is due in part to habitat characteristics, we expect support for models including two estimates of *Pi*, one for each habitat type. Detectability declines with distance, which we hypothesize contributes to heterogeneity of detections. Models incorporating distance therefore represent competing hypotheses with those incorporating unknown heterogeneity. We hypothesized detectability would differ from one year to the next (Norvell et al. 2003) and that detectability would decline with Julian date and time since sunrise (Farnsworth et al. 2002).We evaluated support candidate models using Akaike's information criterion corrected for small sample size (AIC_c). Models were ranked according to the ΔAIC_c from lowest to highest (Burnham and Anderson 2002).

Methodological comparison.— For each species, we evaluated support for detection probabilities and compared estimates of abundance derived from the most supported model for each method. We assessed the influence of differential detectability on the precision of estimates of abundance, and the results of these effects on inferences about relative population densities. Lastly, we compared densities of our focal species in the two study habitats, and to results available in the literature.

Results

We surveyed 227 point counts; 96 in plantation forest, and 131 in native forest. We detected an average of 2.18 (1.99 – 2.38) Acadian Flycatchers per point in native forest, and 1.51 (1.31 – 1.71) per plantation point, 1.15 (0.95 – 1.34) prothonotary warblers per native point, and 0.49 (0.33 – 0.65) per plantation point, and 2.88 (2.64 – 3.12) indigo buntings per native point, and 3.42 (3.17 – 3.66) per plantation point. Truncation of the top 10% of detection distances (Buckland et al. 2001) resulted in effective sampling radii of 95 m for Acadian Flycatcher, 94 m for Indigo Bunting, and 98 m for Prothonotary Warbler.

Distance sampling analysis.—The most supported model for all species in the analysis of detection functions by distance was the uniform key. The simple polynomial adjustment was supported for Acadian Flycatcher and the cosine adjustment was supported for the prothonotary warbler and indigo bunting (Table 2-2). Program Distance does not allow analysis of covariate data with uniform keys. The best model for inclusion of covariate data varied by species. Acadian Flycatcher data most supported a half-normal key with hermite polynomial expansion (Table 2-2). The hazard rate key was most supported for both the prothonotary warbler and indigo bunting, the former with a simple polynomial expansion, and the latter with a cosine expansion (Table 2-2).

The most supported model in the covariate analysis for Acadian Flycatcher remained the uniform key with a simple polynomial expansion (Table 2-4). There was considerable model selection uncertainty, and several temporal covariate models received some support. The most supported covariate model for prothonotary warbler included the year and Julian date terms, and received far more support than any other model ($w_i = 0.405$). The best indigo bunting covariate model included only the year term ($w_i = 0.197$). All other indigo bunting models receiving support also included the year term (Table 2-4).

Table 2-4. Most supported candidate models (ΔAICc < 2.0) used to evaluate detection probability as a function of distance for each species derived from covariate analysis in Program Distance. Covariates include Julian date, year of count, minutes since sunrise, and forest type.

Species	Model		K	AIC_c	$\Delta\ \text{AIC}_c$	w_i
ACFL	Uniform_simple polynomial		1	3475.707	0	0.213447
	Half-normal_hermite polynomial	Julian	2	3476.387	0.679932	0.151931
	Half-normal_hermite polynomial	Year+Julian	3	3477.404	1.697021	0.091366
	Half-normal_hermite polynomial	Year	2	3477.507	1.800049	0.086779
	Half-normal_hermite polynomial	Minutes	2	3477.54	1.833008	0.085361
	Half-normal_hermite polynomial	Type	2	3477.666	1.958984	0.08015
			K	AIC_c	$\Delta\ \text{AIC}_c$	w_i
INBU	Hazard rate_cosine	Year	3	5796.128	0	0.197044
	Hazard rate_cosine	Year+Type	4	5796.369	0.241211	0.174657
	Hazard rate_cosine	Year+Time+Type	5	5797.004	0.875977	0.127159
	Hazard rate_cosine	Year+Time	4	5797.498	1.370117	0.099322
	Hazard rate_cosine	Year+Julian	4	5797.753	1.625	0.087438
			K	AIC_c	$\Delta\ \text{AIC}_c$	w_i
PROW	Hazard rate_Cosine	Year+Julian	4	1627.525	0	0.404531

Recapture and removal analyses.— During the first stage of analysis, heterogeneity models always received overwhelming support. The most supported traditional removal models for Acadian Flycatchers and prothonotary warblers included differences in detectability by habitat, while the most selected model for indigo buntings did not (Table 2-5a). In behavior-removal models for all species, the model including only one heterogeneity mixture across both habitat types received greater support than the model including different mixtures in each habitat. The differences in deviance between the 1 *Pi* and 2 *Pi* heterogeneity models were negligible, further supporting the hypothesis that heterogeneity does not differ by habitat. Habitat effects were included in the best behavior model for Acadian Flycatcher, but not for prothonotary warbler or indigo bunting (Table 2-5a).

The most supported recapture model for Acadian Flycatchers included a single set of heterogeneity mixtures across habitats, and an effect of habitat on detection. The most selected recapture model for prothonotary warbler incorporated different heterogeneity mixtures for each habitat (and therefore a habitat effect). For indigo bunting, the most selected recapture model included a single heterogeneity term and no effect of habitat on detection probability.

In stage two of the analyses, in all cases, models incorporating radial distance as a covariate received support, and models excluding distance received essentially none (Table 2-5b). Detection decreases with distance and confidence limits for effects of distance do not overlap zero in any model.

Table 2-5. Most supported removal and recapture model structures (ΔAICc < 2.0) for evaluating detection probability of focal species arranged by analysis type for each species. In first stage of analysis we selected the best intercept model for each analysis type and present only the best stage one model for each species-analysis pair below. In stage two we evaluated support for the intercept and all combinations of additive covariate models.

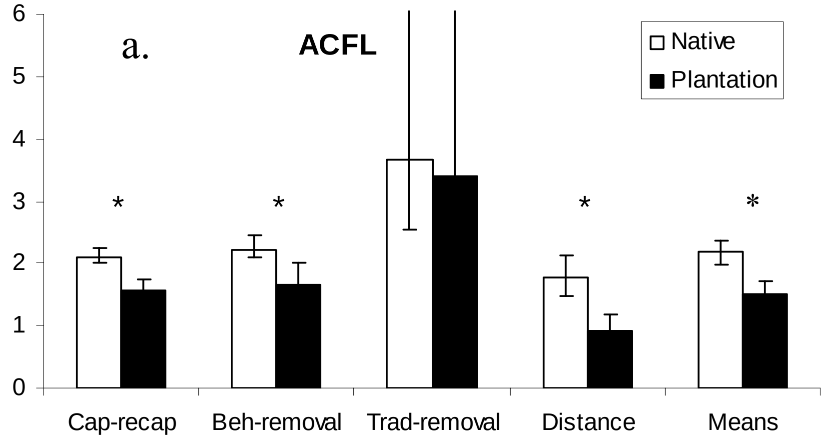
Species	Model		K	AIC$_c$	Δ AIC$_c$	w_i
	Traditional-removal					
ACFL	Mh1_Hab c=0	1.00	4	981.80	0.00	0.55
PROW	Mh1_Hab c=0	1.00	4	449.42	0.00	0.38
INBU	Mh1_NOHab c=0	1.00	3	1515.37	0.00	0.66
	Behavior-removal					
ACFL	Mbh1_Hab	1.00	5	2434.79	0.00	0.45
PROW	Mbh_NOHab	1.00	4	1101.28	0.00	0.36
INBU	Mbh_NOHab	1.00	4	3969.96	0.00	0.65
	Recapture					
ACFL	Mh1_Hab	0.00	4	2453.59	18.80	0.00
PROW	Mh2_Hab	0.02	5	1108.76	7.48	0.01
INBU	Mh_NOHab	0.00	3	3991.86	21.89	0.00
	Traditional-removal					
ACFL	Mh1DJ_Hab c=0	1.00	6	972.22	0.00	0.34
	Mh1DJM_Hab c=0	0.87	7	972.50	0.27	0.30
PROW	Mh1DY_Hab c=0	1.00	6	442.63	0.00	0.35
	Mh1D_Hab c=0	0.73	5	443.25	0.63	0.25
	Mh1DJ_Hab c=0	0.40	6	444.46	1.83	0.14
	Mh1DJY_Hab c=0	0.39	7	444.50	1.88	0.14
INBU	Mh1DY_NOHab c=0	1.00	5	1509.80	0.00	0.22
	Mh1D_NOHab c=0	0.80	4	1510.23	0.43	0.17
	Mh1DJY_NOHab c=0	0.62	6	1510.74	0.94	0.14
	Mh1DJ_NOHab c=0	0.51	5	1511.14	1.34	0.11
	Mh1DJYM_NOHab Global	0.45	7	1511.41	1.61	0.10
	Mh1DM_NOHab c=0	0.38	5	1511.73	1.93	0.08
	Behavior-removal					
ACFL	Mbh1D_Hab	1.00	6	2409.45	0.00	0.26
	Mbh1DJ_Hab	0.78	7	2409.95	0.50	0.21
	Mbh1DJY_Hab	0.55	8	2410.66	1.21	0.14
	Mbh1DM_Hab	0.49	7	2410.89	1.43	0.13
	Mbh1DY_Hab	0.37	7	2411.43	1.98	0.10
PROW	Mbh1D_NoHab	1.00	5	1088.84	0.00	0.31
	Mbh1DJ_NoHab	0.48	6	1090.29	1.46	0.15
	Mbh1DM_NoHab	0.47	6	1090.33	1.49	0.14
	Mbh1DY_NoHab	0.41	6	1090.62	1.78	0.13
INBU	Mbh1D_NoHab	1.00	5	3922.30	0.00	0.18

	Mbh1DY_NoHab	0.98	6	3922.34	0.04	0.18
	Mbh1DM_NoHab	0.97	6	3922.36	0.06	0.17
	Mbh1DJM_NoHab	0.90	7	3922.51	0.21	0.16
	Mbh1DJ_NoHab	0.75	6	3922.88	0.59	0.13
	Mbh1DJYM_NoHab	0.55	8	3923.51	1.21	0.10
	Mbh1DJY_NoHab	0.43	7	3923.98	1.69	0.08
		<u>Capture-recapture</u>				
ACFL	Mh1DJ_Hab	1.00	6	2425.29	0.00	0.27
	Mh1DJY_Habc	0.79	7	2425.76	0.48	0.22
	Mh1D_Hab	0.65	5	2426.15	0.86	0.18
	Mh1DJM_Hab	0.39	7	2427.17	1.88	0.11
PROW	Mh2DJY_Habd	1.00	8	1096.36	0.00	0.28
	Mh2D_Hab	0.72	6	1097.03	0.67	0.20
	Mh2DJ_Hab	0.63	7	1097.28	0.92	0.17
	Mh2DJYM_Habe	0.38	9	1098.30	1.94	0.10
INBU	Mh1DY_NOHab	1.00	5	3941.26	0.00	0.20
	Mh1D_NOHab	0.95	4	3941.38	0.11	0.18
	Mh1DM_NOHab	0.94	5	3941.40	0.13	0.18
	Mh1DJM_NOHab	0.71	6	3941.96	0.70	0.14
	Mh1DJ_NOHab	0.64	5	3942.16	0.89	0.13
	Mh1DJYM_NOHab	0.47	7	3942.77	1.51	0.09
	Mh1DJY_NOHab	0.42	6	3943.01	1.74	0.08

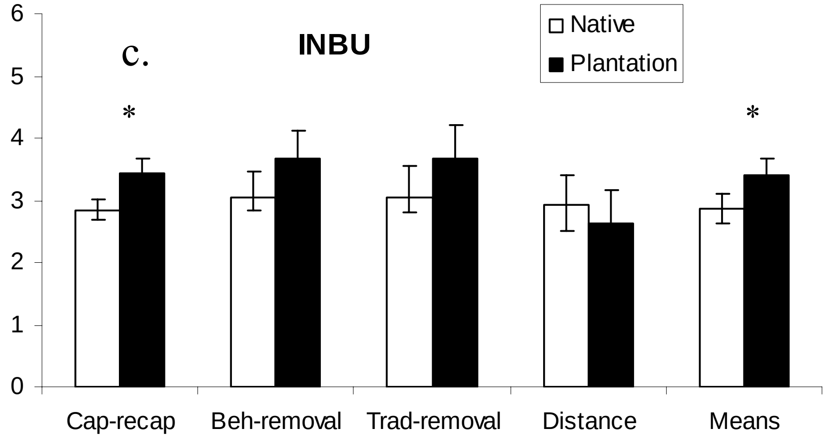
Confidence limits for model coefficients for temporal covariates overlapped zero in most models for all species. Julian date was the only exception, and this effect appeared inconsistent across models in a given set (Table 2-5b). There was a significant effect of Julian date for Acadian Flycatcher in the traditional removal data set, and in one model out of three (but not the top model) containing the effect in the recapture set. The prothonotary warbler recapture data set included three supported models with the Julian effect, and two of these showed significant influence of date. The indigo bunting data provided no support for temporal effects in any model. Moderate model selection uncertainty was evident in all analyses (Table 2-5b).

Abundance.—Excepting traditional removal, abundance estimates were generally similar among methods for each species. Estimates based on traditional removal models were larger and had much wider 95% confidence limits, for Acadian Flycatchers and prothonotary warblers (Figure 2-2). Prothonotary Warblers consistently had the lowest relative abundances of the three species, and indigo buntings had the highest abundances.

Figure 2-2. Birds per point for Acadian Flycatcher, prothonotary warbler, and indigo bunting from analyses of point count data via five different methods in two forest types. Asterisks indicate non-overlapping 95% confidence intervals.


a.
ACFL
Native
Plantation
0
1
2
3
4
5
6
*
*
*
*
Cap-recap
Beh-removal
Trad-removal
Distance
Means


b.
PROW
Native
Plantation
0
1
2
3
4
5
6
*
*
*
*
Cap-recap
Beh-removal
Trad-removal
Distance
Means


c.
INBU
Native
Plantation
0
1
2
3
4
5
6
*
*
Cap-recap
Beh-removal
Trad-removal
Distance
Means

Acadian Flycatcher abundance was greater in native than plantation forest, based on all methods but confidence intervals overlapped using the traditional removal method (Figure 2-2a). Similarly, abundance estimates for prothonotary warbler based on recapture, behavior-removal, distance, and means methods were significantly greater in native forest (Figure 2-2b). The abundance estimate for prothonotary warblers in plantation forests was greater than the native forest estimate, based on the traditional removal model, but the confidence interval around the plantation estimate was exceptionally wide (Figure 2-2b). The native forest estimate was more similar to estimates based on other models, and confidence intervals were somewhat narrower than for the plantation estimate (Figure 2-2b).

Discussion

Methodological comparison

All methods provided comparable estimates of avian abundance, but support for differences in abundance between habitats varied among methods. This likely depended not only on the amount of data, but also on the structure of data. For example, the traditional removal method performed poorly with our Acadian Flycatcher and Prothonotary Warbler data as demonstrated by extremely wide confidence intervals and higher abundance estimates. We had fewer detections of each of these species than Indigo Buntings, but the lack of precision likely results from high numbers of initial detections in late intervals. Removal methods require that new detections decline over subsequent intervals. Species that sing intermittently may not be detected until late in the count period simply by chance. Our prothonotary warbler data provides an important example. Given the breeding requirements of this species (mature forest, generally with some standing water and previously excavated cavities) and structure of plantations (younger trees, limited water availability, little prior woodpecker activity) we expected lower abundance of this species in plantation forests. Our daily observations while nest searching and conducting point counts supported this hypothesis. However, the traditional removal method suggests higher abundance in plantations. We believe singing behavior of this species influenced our results. Males may be quiet for extended periods. However, when an individual sings, nearby males often readily counter-sing. In native forests, where there are more prothonotaries and they are more detectable (Table 2-6) the traditional removal method provided estimates comparable (though the confidence interval was wider) to the other methods (Figure 2-2b). Similarly, although traditional removal method abundance point estimates for Acadian Flycatcher still indicate higher abundance in native forest, the higher estimates, relative to other methods, and the wide confidence limits likely result from lower detectability (as modeled by other estimation methods and discussed below; Table 2-6) and the tendency for this species to maintain silence for extended periods, and counter-sing when a neighboring male sings. Traditional removal models should only be considered in situations where the species being surveyed are relatively common and sing often and are therefore highly detectable and likely to be detected early in the count period. Otherwise, confidence intervals are likely to be so wide that little inference can be made regarding the populations in question.

In all cases, methods incorporating the probability of recapture, a behavioral response (change in detection probability from initial to subsequent intervals), and mean-birds-per-point methods produced similar point estimates and confidence intervals. Incorporating recapture or behavior components to point count methods addresses bias that may be associated with uncorrected count data, by assessing detectability (McCallum 2005). It is therefore interesting that our abundance estimates were very similar for model-based and unadjusted count data. This may result from the fact that our focal species generally had a high probability of detection. Species with low detectability, or species for which a large proportion of the population is difficult to detect will likely bias conclusions. We therefore agree with others who encourage splitting point counts into multiple, short duration intervals (Farnsworth et al. 2005, Alldredge et al. 2007a), particularly if a study will focus on only a few species.

Table 2-6. Removal and recapture detection probabilities and (standard errors) based on the best model for each species, forest type, and analysis. Detection group refers to easy and difficult to detect heterogeneity groups. *Pi* is the probability that a randomly selected individual will be a member of the difficult group. Estimates for *Pi* are the same for each model-by-forest pairing except in the Prothonotary Warbler capture-recapture analysis where heterogeneity groups differed by forest type.

	Detection group	Trad. Removal	Beh. Removal	Cap.-recapture
ACFL				
Plantation				
	easy	0.66 (0.098)	0.80 (0.057)	0.85 (0.035)
	diff	0.03 (0.020)	0.27 (0.050)	0.35 (0.046)
		Pi = 0.39 (0.099)	*Pi* = 0.32 (0.051)	*Pi* = 0.38 (0.051)
Native				
	easy	0.81 (0.057)	0.85 (0.040)	0.88 (0.025)
	diff	0.06 (0.036)	0.34 (0.043)	0.41 (0.039)
		Pi = 0.39 (0.099)	*Pi* = 0.32 (0.051)	*Pi* = 0.38 (0.051)
PROW				
Plantation				
	easy	0.42 (0.093)	0.80 (0.111)	0.82 (0.058)
	diff	0.002 (0.002)	0.28 (0.085)	0.17 (0.088)
		Pi = 0.17 (0.068)	*Pi* = 0.32 (0.105)	*Pi* = 0.446 (0.100)
Native				
	easy	0.99 (0.008)	0.80 (0.111)	0.95 (0.031)
	diff	0.28 (0.064)	0.22 (0.085)	0.45 (0.038)
		Pi = 0.17 (0.068)	*Pi* = 0.32 (0.105)	*Pi* = 0.227 (0.059)
INBU				
Plantation				
	easy	0.98 (0.042)	0.74 (0.030)	0.81 (0.019)
	diff	0.30 (0.039)	0.24 (0.038)	0.32 (0.036)
		Pi = 0.30 (0.048)	*Pi* = 0.47 (0.041)	*Pi* = 0.49 (0.040)
Native				
	easy	0.98 (0.042)	0.74 (0.030)	0.81 (0.019)
	diff	0.30 (0.039)	0.24 (0.038)	0.32 (0.036)
		Pi = 0.30 (0.048)	*Pi* = 0.47 (0.041)	*Pi* = 0.49 (0.040)

A source of potential bias influencing the decision to use recapture or behavior-removal methods is the need to track individuals to avoid over-counting. Such tracking directly influences the probability of subsequent detections, suggesting the use of behavior-removal models over recapture models. AIC strongly supported this conclusion as demonstrated by the substantially lower AIC_c value for behavior models compared to recapture models (Table 2-5). The wider confidence intervals around estimates based on behavior-removal models (relative to those around recapture model estimates) are due to a lower probability of detection (Table 2-6). This is best demonstrated by the poorest performing models. Specifically, in all instances where recapture and removal model estimates have wide confidence intervals (Figure 2-2), the probability of detection of the difficult to detect birds is < 0.10. Very low detection probabilities in these cases not only reduced the precision of the abundance estimate, but also created the potential for erroneous conclusions about the populations in question (Figure 2-2b – traditional removal method). Based on these findings, researchers using similar modeling methods need to be aware of this strong source of bias, and carefully assess not only the detection probabilities but the probability of birds being in the difficult to detect group (i.e. the *Pi* parameter in Program MARK mixture models).

We specifically wanted to compare estimates based on removal and recapture models to evaluate how the additional capture information would effect results. We therefore based a second-stage covariate analysis on both the best model from the stage-1 analysis (always a behavior-removal model) and on the best capture-recapture model from stage-1, even though the behavior removal model received much more support in the first stage. In general, the recapture models performed similarly to the behavior-removal models and had slightly narrower confidence intervals. Ultimately however, behavior-removal models incorporating heterogeneity were the best supported device for comparing habitat specific densities based on our data. Alldredge et al. (2007a) also found strong support for heterogeneity, and noted, as in our study, that fuller models were often selected over simpler ones. In practice it is simple to compare estimates and confidence intervals, and to generate abundance estimates based on the "best model" or any other biologically relevant model of interest. It is critical that researchers interpret their results within the context of both a species' biology and the effects of the point count protocol. In this case, the need to track individual birds over the entire count period to avoid double-counting necessitates using the behavioral response models.

We believe our data demonstrates the dangers of relying on distance data alone to generate detection probabilities for a species (Alldredge et al. 2007b). In comparison to estimates based on removal or recapture, the distance-based lower estimates for Acadian Flycatcher in both forest types, and indigo bunting in plantations, and the higher estimates for Prothonotary Warbler in native forests likely arise from imprecise estimates of distance. The fact that songbird abundance surveys largely rely on auditory cues, and the concomitant lack of visual verification means that there is considerable uncertainty inherent in the data. Recent work has demonstrated high levels of bias in distance estimates for even moderately experienced counters (Alldredge et al. 2007b). Surveyors likely have trouble consistently estimating distances since individual birds vary in detectability due not only to variable distance and orientation, but to vegetative cover and height as well. In our case, Acadian Flycatchers and indigo buntings can appear deceptively far away, due to the high attenuation of their calls by dense vegetation, while prothonotary warblers have loud, carrying calls and often inhabit (in our study sites) older forest sites with fairly open understory which does little to attenuate calls. We agree with others who have questioned the use of distance data as a basis for calculating detection probability, particularly when other methods are available that remove this important source of bias (Norvell et al. 2003). There are, however, good reasons for collecting distance data. Alldredge et al. (2007a) found that incorporating distance as a linear additive effect resulted in lower AIC_c values. Our results strongly support this finding. Models not containing distance as a covariate did not receive substantial support, and were not included in the top model set (Table 2-5). Concerns about the influence of biased distance estimates may be mitigated by collecting distance data as precisely as possible in the field, and then binning the data into discrete radial distance categories for analysis (Buckland et al. 2001).

Habitat comparison

As expected, we found higher densities of Acadian Flycatchers and prothonotary warblers in native than in plantation forests. However, prothonotary warblers were regularly encountered in plantation forests where natural or artificial cavities existed, suggesting that this species would utilize plantations if suitable nesting sites exist (Twedt and Henne-Kerr 2001). Petit (1999) reported that densities in box provisioned river habitat were higher than elsewhere. Our density estimates based on behavior-removal models for this species of 0.38 (95% CI: 0.34 – 0.50) in native and 0.17 (95% CI: 0.16 – 0.23) in plantation forests are within the range reported for this species: 0.075 – 1.085

birds/ha throughout Illinois; 0.6 territories/ha in southern Illinois; 1.2 males/ha in western Tennessee (Petit 1999). Our densities appear to be somewhat lower than found in some studies, which likely relates to small patch size and the lack of standing water in many of our sites. It is notable that two of our sites hosted multiple pairs of warblers during a wet year, when standing water was abundant, but either had reduced territory numbers or completely lacked prothonotary warblers during dry years (M.S. Pruett, pers. obs.). Petit (1999) reported that standing water (at least temporary) was a nearly universal feature at prothonotary warbler nest sites.

Our Prothonotary Warbler results may have been confounded by the presence of nest boxes in some plantation areas. Nine plantation plots were provisioned with 490 milk carton nest boxes (Twedt and Henne-Kerr 2000) in the spring of 2004 to determine the response of cavity nesters to the addition of boxes in plantations. A flood during the 2004-2005 winter completely destroyed over 65% of the boxes. An additional 10-15% were largely or wholly unavailable for bird utilization by the beginning of the 2005 breeding season due to over-winter habitation by mice. The boxes were completely filled with fine material for insulation and no birds were found using these boxes. By the 2006 breeding season, when we initiated point counts, less than 5% of the boxes remained throughout the study area, and many of these were only tattered remains. One bird was found nesting in a box in 2006 and protecting another, partially intact box, at the edge of his territory. No other active boxes were found during the point count period. However, if birds were present in the plantation due to remaining but unobserved nest boxes, our density estimates for this species in plantation forests would be biased upward. Based on our observations of nest box remnants at the time of the point counts we do not believe this problem to exert substantial influence on our results.

Acadian Flycatchers were more common in plantations than prothonotary warblers, suggesting a slightly broader availability of appropriate habitat structure. According to Whitehead and Taylor (2002) this species “requires relatively undisturbed mature forest” but has been reported in 35 – 50 year old pine plantations as well. Our research demonstrates Acadians can have equal reproductive success in hardwood plantations of appropriate structure (Pruett 2008). Other recent work also has suggested more flexibility in Acadian Flycatcher habitat selection than the older literature indicates (Hazler et al. 2006).

While Acadians were generally more widespread in plantations than prothonotaries, it also appeared to select certain structural components more often than not. Acadians were not often found nesting directly in the plantation cottonwoods themselves, but in masses of vines hanging in the subcanopy of the trees. Where this structure exists, Acadians are regularly found and to be expected. In younger stands, or similarly aged stands without conspicuous vine growth, they are typically far less likely to occur (M.S. Pruett – personal obs.). As with prothonotary warblers, our Acadian Flycatcher native and plantation forest densities, 0.78 males/ha (95% CI: 0.74 – 0.87) and 0.59 (95% CI: 0.54 – 0.71) males/ha respectively, are within the reported range for this species in other areas. High estimates (1.8/ha) occurred in West Virginia, while the lowest densities (0.12/ha) were in climax oak-hickory forests in Georgia (Whitehead and Taylor 2002). Higher densities appear to be associated with bottomland (1/ha in Maryland and Tennessee; 0.64/ha in eastern Arkansas) than in upland forests (0.39/ha in

Arkansas; 0.26 – 0.30/ha in Missouri). Our native forest estimates remain similar when compared to these bottomland specific values, but cottonwood plantation estimates are more similar to reclaimed strip-mine bottomland forest densities in south-central Indiana (0.56/ha) (Whitehead and Taylor 2002) which may relate to some structural aspect of the Indiana forests.

Differences in indigo bunting density between the two forest types were equivocal. The traditional means and recapture methods indicate significantly higher densities of this species in plantations. Both removal methods, while suggesting the same, have overlapping confidence intervals indicating non-significant differences (Figure 2-2) thus illustrating more conservative inferences to be drawn regarding differences between habitats. Interestingly, the estimates from traditional and behavior removal methods are almost identical. As noted previously, this is likely the result of the high detectability and often near-constant singing of this species. Most individuals are detected in the early intervals, resulting in substantially narrower confidence intervals. Finally, the distance method suggests a nonsignificantly higher density of this species in native forest. Based on the congruence of all other methods, and our own field observations, we feel this result is inaccurate for the reasons discussed above. Most prominently, the relatively open understory of many plantation patches may have little attenuating effect on the calls of distant birds, causing distance estimates for non-visual detections to be biased low. We often walked towards distant birds to obtain more accurate estimates of their distance from the point. Birds sometimes flushed away, or moved toward the counter as if to determine the source of disturbance. Such movements, if undetected and accounted for, could also bias the resulting estimates.

Our behavior-removal model estimates for indigo buntings, 1.08/ha (95%: 1.00 – 1.22) in native and 1.30/ha (95% CI: 1.21 – 1.46) in plantation are actually higher than most available estimates for this species. Very lower density estimates of less than 0.1 birds/ha (1.19/ha in shrub and hedge habitat) occurred in Illinois. Estimates in West Virginia, southern Michigan, and North Dakota were 0.38, 0.35, and 0.28 respectively. Our estimates in both habitats therefore appear to be among the highest reported for this species. Given low nest survival on our study sites, and the high densities we found, it is possible that fragmented forests in the heavily altered floodplain forests of southern Missouri may act as ecological traps (Battin 2004).

The original context of this research was to assess whether monoculture paper pulp plantations along the Mississippi river were comparable to native forests as breeding habitat for a variety of forest nesting passerine birds. The extreme loss of bottomland habitat in this region certainly contributed to regional declines in many species. The original bottomland forests supported one of the most highly diverse communities in North America (Sharitz and Mitsch 1993, Rudis 1998). Plantation forests are structurally much simpler, and consequently support reduced faunal diversity. It is therefore unrealistic to expect these forests to function as equals to native systems. However, understanding their value to wildlife that do use them is important for understanding the functioning of the Mississippi Alluvial Valley as a whole for wildlife conservation. We feel therefore that our study fills an important gap in this regard.

Our measures of nest survival did not differ substantially between native and plantation forests (Pruett 2008). Taken alone this metric would suggest that the habitats are relatively equal in quality to the species breeding there. However, overall productivity of each forest type, measured purely as the number of individuals produced per forest type, will be higher in higher density habitats. Acadian Flycatchers and prothonotary warblers, generally thought of as mature forest specialists, produce more individuals in native than plantation forests. Indigo Buntings, much more general in their nesting requirements, may actually produce more offspring in plantation forests. At the very least they appear to produce equally in the two forest types.

When considering the function of plantations in this landscape, the fact that they are utilized by native forest nesting species, and that reproductive success is comparable, means that plantations provide a useful alternative where very little native structure exists, particularly as a location where "extra" birds can breed. However, the lower densities achieved in plantations mean that we should not rely on them as a core component of songbird conservation. The real value may be that they increase overall forest cover in the landscape and may mitigate some negative effects of the substantial historic alteration of this region (Pruett 2008).

If we only measured one metric to assess relative habitat quality (reproductive success or density) our results would only have captured part of the story. The more traditional metric (since Van Horne 1983), reproductive success, indicated no difference between the two forest types. For managers interested in the value of alternate habitats, acknowledging differences in how habitats influence the density of breeding populations is as important as knowing relative habitat quality, based on reproductive success. As Bock and Jones (2004) warned, density in this highly disturbed landscape failed to match reproductive success. However, in this instance, density provides insights into habitat differences that reproductive success alone does not illuminate.

Management Implications

Our results suggest that although unadjusted point count data is potentially biased because it fails to account for variable detectability, estimates obtained from it and methods such as capture-recapture are similar when sample sizes are reasonably large and when species have a high probability of detection. When many species are being monitored however, accurate data collection for capture-recapture analysis is likely to be untenable. Collecting capture-recapture data is an intensive activity, due to the need to avoid double-counting of individuals, and as such managers may opt to focus point count efforts on a small suite of species with inherently high or at least moderate detectability. Concentrating on species of conservation concern, whose habitat needs coincide with a larger community, will enable deeper exploration of the demography of a particular species, while revealing how various factors of alternate habitats influence the population growth and maintenance.

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Chapter 3 - Nest Predators in Plantation and Native Forests in the Mississippi Alluvial Valley

Introduction

Predation is a substantial pressure on nesting birds (Wilcove 1985, Sabine et al. 2005, Thompson 2007). To gain insight regarding how predation may influence breeding birds, knowledge of the specific predators in a system is critical, as is acknowledging temporal patterns of nest predation (Stake et al. 2005). Traditional methods of identifying predators relied on evidence at the nest post-predation (nest damage, tooth/claw marks on plasticine eggs, etc.) or anecdotal evidence (known or suspected predators active in the nest area) (Best et al. 1980), and fortuitous observations of predation events (James et al. 1983, Hazler et al. 2004). Efforts to more rigidly assess the predator community quite naturally turned to cameras as a means of collecting more and better data (Picman 1987).

Video surveillance of songbird nests has substantially enhanced our knowledge of a critical period in the life history of most birds (Thompson 2007). Researchers have documented a wide variety of nest predators (Purcell and Verner 1999, Pietz and Granfors 2000a, Pietz and Granfors 2000b), observed important interactions and behaviors at the nest (Fuller and Booms 2003), enlarged our understanding of predator behavior (Bradley and Marzluff 2003, Stake et al. 2005), and documented differences in predation between habitats and over time (Picman and Schriml 1994, Williams and Wood 2002, Thompson and Burhans 2003). Cameras have also been used to demonstrate serious potential biases of artificial nest studies (Thompson and Burhans 2004). The future use of video at songbird nests is assured as new technologies are developed and increase the ease of deployment, power efficiency, and the amount of data that can be obtained (Pierce and Pobprasert 2007).

Our objectives were to develop and test an inexpensive time-lapse video system to be used in the study of passerine bird nesting ecology, and to use this system to determines sources of nest failure and to identify predators in bottomland hardwood and cottonwood plantation forests in southeast Missouri.

Materials and methods

We conducted this study during the breeding seasons of 2004-2006 in the bottomland hardwood forests and cottonwood plantation forests along the Mississippi river in the southeastern Missouri (Mississippi and New Madrid Counties) and on two small Kentucky islands comprising parts of Carlisle and Hickman counties. Publicly owned study areas included Donaldson Point and Ten Mile Pond Conservation Areas (Missouri Department of Conservation) and Big Oak Tree State Park (Missouri Department of Natural Resources). The remainder of our study was conducted on private land.

The native forest has largely been harvested for lumber in the past and is in various stages of secondary growth and development. A small section of Big Oak Tree State Park is the only representative old growth forest remaining in southeastern Missouri. Native forest understory tends to be relatively open in low lying areas where intermittent flood waters reduce flood intolerant plants, but can be densely vegetated from the ground to subcanopy in tree-fall gaps and along edges. Cottonwood (*Populus deltoides*) is the most commonly planted tree in southeast Missouri plantations (M. S. Pruett pers. obs). Plantation understory is often uniformly open in the early season, and progressively denser as seasonal herbaceous plants and vines increase through the growing season. Ragweed (*Ambrosia trifida*), poison ivy (*Toxicodendron radicans*), and rough cocklebur (*Xanthium strumarium*) form a dense understory, often to >2 m deep in older cottonwood stands (> 7 yrs). The study area is bounded on the east by the Mississippi river. Row cropping of soybeans, corn, millet, and sunflowers now represents the predominate regional land use.

As part of a larger study on the effects of plantation forestry on native fauna (Papon 2002), sixteen four mi^2 blocks were randomly selected from over 250 possible blocks in the Missouri MAV. We used 10 of these sites in the first year and nine in the remaining years. Within these four mi^2 areas, the sizes of the actual forest patches are varied and depend on pre-existing forest conditions and management plans (Table 3-1).

Table 3-1. Locations, forest type, patch size and percent forest cover for avian point counts in southeast Missouri, 2006-2007. N = native forest, P = plantation. Patch size is presented in hectares. Percent forest cover is within a 5 km radius around the count site.

Site	Forest type	Patch size	% Forest
Big Oak	N	412.70	16.99
Corse	N	89.54	6.25
Donaldson	N	2531.67	39.45
Gertrude	N	81.28	8.90
Island 3	P	413.30	30.98
Medlin	N	68.17	14.40
Ten Mile	N	731.52	13.50
Winchester	P	721.10	45.75
Wolf	P	1457.43	30.85

As part of our nest survival study (Pruett 2008), we located and monitored nests of three forest nesting passerines: Acadian Flycatcher (*Empidonax virescens*), prothonotary warbler (*Protonotaria citrea*), and indigo bunting (*Passerina cyanea*). We visited nests at least every third or fourth day to monitor survival. We selected nests of these and several other species found during the course of the study (Table 3-2) for continuous video monitoring, and began taping as soon as possible during the nesting cycle, after the initiation of incubation. To avoid influencing nest fate, we selected nests that could be monitored without removing or modifying the surrounding vegetation, which limited the nests available for continuous observation.

Camera system

Our system consisted of easy to obtain weather-resistant, infrared (IR) security camera, a time-lapse, 12-volt video tape recorder, and a 12 volt deep cycle marine battery purchased locally. Due to initial problems, we cut tops off of plastic drink bottles and fitted plastic hoods to some cameras to reduce the likelihood of rain water collecting on the front glass of the camera. The cameras contained photocells which controlled IR illumination and reduced battery usage during daylight hours. Infrared diodes provided illumination adequate for viewing at distances up to 20 feet, though we never deployed a camera that far from a nest. We chose a black and white camera to reduce cost and because night-time images would essentially be black and white anyway under IR illumination. We used IR cameras that illuminated at 850-nm.

Table 3-2. Number of nests monitored in native and plantation forests for each species and number of each predator observed at each species' nest in southeastern Missouri, 2004-06.

	Nests in		Predators observed			
Species	Native	Plantation	Hawk	Snake	Woodpecker	BHCO
Acadian Flycatcher	21	17	1		1[a]	
indigo bunting	11	38	2	3		1
prothonotary warbler	15	5		1	1	
blue-gray gnatcatcher	1	6		1[b]		1
Carolina wren	3	1		1		
wood thrush	0	1		1		
white-eyed vireo	1[c]					
Total	52	68	3	7	2	2

[a] unsuccessful attempt – force fledge

[b] suspected

[c] fledged

We removed the standard, wide-angle lens the cameras were equipped with and installed a 16mm micro lens, which gave us considerably greater magnification of the nest, and allowed placement of the camera farther from the nest. Fine focus was possible by opening the camera and turning the lens in or out to the appropriate distance.

We use a variable speed, time-lapse, VHS video tape recorder capable of continuous recording for up to 960 hours at the lowest image capture rate. We operated the recorder at approximately four frames per second (one image every 0.22 second), representing a trade-off between increasing the recording period between battery changes, and decreasing the potential of missing an event due to a slow rate of capture. Given an adequate power supply, this rate captures 78 hours of footage on a standard T-120 video tape.

The recorder was housed in a medium sized (#1500 or #1550) Pelican brand weatherproof case. We modified each case by cutting a one inch notch in the lip to allow the cables to pass through the wall. We maintained most of the weatherproof nature of the original case by applying foam weather stripping to the notch. During the first season we used compressible foam inside the case to hold and protect the VCR during transport over sometimes rough terrain. Due to overheating issues with the system, in subsequent seasons we substantially reduced the foam padding and utilized Velcro straps attached to the bottom of the case to secure the VCR with some success.

We removed the car-lighter style power plug on the VCR power cable and replaced it with individual alligator clips for direct attachment to the battery. Our power supply for each system was a rechargeable 12V marine deep-cycle battery rated at between 800 and 1000 cranking amps, 110 or 115 amp hours, and a 180 reserve capacity.

Batteries and tapes were changed every 3 days. We chose a VCR with an onboard power-out port allowing us to connect the camera to the VCR and the VCR directly to the battery.

Camera deployment

We attempted to begin recording during incubation, but this was not always feasible due to variation in when nests were found and availability of systems. We placed cameras at nests of forest passerine birds breeding in native and plantation forests (Table 3-2). We attached cameras to nearby vegetation with clamps or mounted them on poles driven into the soil. We used 15.25 m combination power and video cables to connect the camera to the VCR. We attempted to monitor both low shrub and sub-canopy nests to test the effectiveness of the cameras for different tasks and sample from a variety of potential predator taxa. The distance between a nest and the camera varied from one to eight meters, but was typically one to three meters. We avoided removing vegetation associated with nest concealment, which limited the number of nests available for monitoring. We did remove vegetation between nest and camera to clear the view if we felt it was not involved in nest concealment. The VCR case was tethered to the trunk of a tree to prevent theft, or the system from floating away during flood events. We covered the battery and VCR case with camouflaged material to reduce visibility to potential predators and to protect against theft.

Results

We monitored 120 nests of seven species with video. Sixty-eight nests (57%) in plantations, and 52 (43%) in native forest were observed. We deployed two cameras during the laying stage, 73 during incubation, and 45 during the nestling period. Sixty-two nests (52%) successfully fledged young, 38 (32%) were depredated, eight (0.07%) were lost in weather related events, five (0.04%) were abandoned, two (0.02%) were trampled by deer, and the fates of five (0.04%) were unknown. Three of the unknown cases resulted from camera removal at the end of the season before the nest cycle was complete.

Twenty-four (63%) nests that were or appeared to have been depredated were missed on cameras. Thirteen of these instances were VCR, camera, or battery failures. Movement of the camera (n=3) or nest (n=8) such that the nest was out of the field of view also generated substantial loss. Three nests were depredated while the camera remained functional, but no evidence was ever found on tape to explain the nest loss.

We identified four nest predators including brown-headed cowbirds (*Molothrus ater*), as well as documenting post-predation visits to nests by mice on two occasions, and a raccoon passing near a previously depredated nest (Table 3-3). Black rat snakes (*Elaphe obsoleta*) were the most common nest predator observed in both habitat types. No depredations by mammals were directly observed, although mice visited nests recently depredated by other predators. Avian predators were red-shouldered hawk (*Buteo lineatus*) and red-bellied woodpecker (*Melanerpes carolinus*). In one instance a hawk of uncertain ID was observed as a blur in two frames at an Acadian Flycatcher nest. This individual was either another red-shouldered hawk or a Cooper's hawk (*Accipiter cooperii*). All avian depredations occurred during daylight, while all mammalian visits to nests were nocturnal. Snake activity was only recorded at night but snakes were visually observed depredating nests during the day.

Field Issues

During the first season, when changing batteries and tapes, we regularly found the system non-functional. Most of these cases occurred on hot days (i.e. > 97°) and we assumed the systems were overheating. In 14 instances we missed a predation event. At other times we simply needed to restart the system and continue monitoring the still active nest. We reduced the incidence of overheating substantially by removing much of the insulating foam inside the case and utilizing larger cases. However, we continued to have similar intermittent problems throughout the course of the study, and we believe the high humidity levels are partially responsible. Non-functional systems would often begin functioning properly when brought into an air-conditioned building and allowed to dry out for a short period of time. In some cases batteries failed. During the first season, three batteries were identified as showing a full charge and draining within hours of deployment, but this problem wasn't accurately diagnosed until it occurred several times because we assumed it was associated with the overheating issue. Labeling of batteries for individual identification, and testing them intermittently throughout the summer and at the initiation of the following year largely rectified this problem.

Table 3-3. Number of video observations of each predator in each forest type, 2004-06, southeast Missouri. Equipment failure and vegetation issues includes only missed depredation/fledge events, not all equipment failures.

Predator	Number of observations in Native	 Plantation
black rat snake	3	4
red-bellied woodpecker	2	
red-shouldered hawk		2
Unk. hawk[a]	1	
BHCO		2
mouse[b]		2
raccoon[c]	1	
Other		
Equipment failure	4	5
Vegetative issues[d]	2	7

[a] Coopers hawk or red-shouldered hawk – only briefly visible before nest dropped out of view of camera.

[b] Mice observed on two occasions visiting a nest after depredation event by another species.

[c] Raccoon suspected at prothonotary warbler nest; not captured on camera due to a camera failure, but tracks around nest substrate and claw marks on trunk support raccoon depredation.

[d] Vegetation either obscured view after camera installation, or nest substrate vegetation failed during predator encounter rendering ID of predator unresolved.

We used IR illuminated cameras to continuously monitor overnight. These cameras are designed to operate at very low light intensity (0.5 lux). We found several situations when lighting was troublesome. Positioning the camera in a southward orientation often resulted in extreme glare, obliterating visibility of the nest. This was true not only when the sun shone directly into the lens, but also when it shone obliquely across the lens from anywhere in front of the camera. A similar problem occurred on a full moon night when the moon passed directly in front of the camera. The high reflectivity of many leaves caused contrast problems when the IR lighting shone directly on them. The extreme reflectance of IR off the leaves would wash out those surfaces, while leaving shadowed areas underexposed. This sometimes meant the nest was nearly invisible at night in some broad-leaved vegetation types (e.g. Poison ivy, *Toxicodendron radicans*).

Our cameras emitted IR illumination at 850-nm, compared to the 950-nm cameras used in some other studies (Pietz and Granfors 2000a, Thompson and Burhans 2003). Viewed from the front, a faint red glow was visible after dark from each 850-nm diode, but not from the 950-nm diodes. Neither camera produced visibly reflected illumination to human eyes. Whether this wavelength is visible to nocturnal predators is uncertain. In one case, a raccoon oriented on the camera apparatus, but then moved away and did not return.

In some cases we tried to monitor nests too far away and couldn’t see the outcome clearly. At the most extreme, a blue-gray gnatcatcher nest was difficult to see against the surrounding vegetation. In other cases the longer distance was associated with trying to maintain a view of Acadian Flycatcher nests at the tips of long, highly flexible branches.

Movement of intervening vegetation and of the nest branch itself often obscured the nest image. There were several cases involving the depredation of a nest when no overt activity was visible on tape. In at least two instances, the predator is only visible briefly, in one or two frames of film, before either carrying the nest out of the field of view or completing the depredation and leaving.

Raindrops on the front glass of the camera during inclement weather sometimes compromised the camera's ability to capture footage. We were able to eliminate all but the worst situations by cutting plastic drink bottles and fixing them to the weather guard provided by the manufacturer. Only in very windy events did this fail to protect the camera lens. It did not however protect lenses from nearby vegetation blowing into the front-piece and leaving water streaks or leaf matter to obscure the image. In such cases we simply removed any potentially troublesome stems and leaves from the area around the front of the camera.

Our study area was part of a large, historically active floodplain. In two instances our sites were flooded while cameras were in place. One camera captured the depredation of a Carolina wren (*Thryothorus ludovicianus*) nest by a snake, followed by the rising of flood waters to several feet and completely covering the battery. Enough excess wire existed between the battery and the case to allow the case to float above the battery and continue running. During that night, a raccoon swam into view, climbed the tree trunk of the previously depredated wren nest, oriented on the camera briefly, then dipped back into the water and swam away. The system continued functioning until the next morning when we arrived and disconnected the leads. In the other instance, the site only flooded to a few inches deep, and the battery terminals and VCR case were still well above the wet-line and functional.

We did notice that after a couple of seasons many of the metal connectors began to rust and had to be replaced. Other electrical issues included gnawing of wires by rodents and short-circuiting of wires due to the strain on connection points when wires cameras were elevated and the wire weight pulled on weak connections. The first we mostly solved by applying a commercially available rodent repellent to the wires at the beginning of the field season, and then again after exposure to rain or flood waters. Short circuits were mended as needed and new connections put in place. To reduce strain on the wires, we generally attached them to tree limbs and branches using plastic “zip” ties so that the weight of the wire rested along its length, and not on the connections which tend to be the weakest points.

Discussion

Even given our small sample size, our findings generally support the idea that snakes are important predators in some communities (Stake et al. 2005, Carter et al. 2007). Thompson and Burhans (2003) reported that only raccoons were more important than snakes in forested habitats in central Missouri. In our study, even though raccoons or their spoor are observed on almost a daily basis we did not record a single depredation by this species. Snakes appear to be relatively common nest predators despite the fact that they are rarely observed. Moreover, several times we observed snake depredations in progress during the course of the study, including the apparent depredation of an adult tree swallow and her eggs, and the consumption of at least four large Baltimore oriole (*Icterus glabula*) nestlings from a single nest. In the case of the oriole depredation, the snake climbed the correct tree, and then navigated directly to the end of the branch containing the nest. This observation suggested that not only are snakes capable of identifying nests as prey items, probably as a result of bird flights to and from the nest (Mullin and Cooper 1998), but that they also are capable of difficult spatial navigation to reach their prey. Kingsnakes (*Lampropeltis* spp.) and garter snakes (*Thamnophis* spp.) were also regularly observed and though not caught on video, may also be nest predators. A kingsnake was observed descending a cottonwood tree, and a garter snake was seen in a shrub near an indigo bunting nest, which was depredated later the same day (all observations: M. S. Pruett).

Although our observations for any individual species are few, it appears that as a group, avian predators are also important in this system. Red-shouldered hawks are fairly common and regularly observed in the larger remnant forest patches and older plantation plots on our sites. Cooper’s hawks are less common, but occur as well, and both probably opportunistically eat eggs and nestlings (Stake et al. 2004, Small 2005). Red-bellied woodpeckers are a common bottomland resident, and have been implicated as important nest predators (Hazler et al. 2004). In addition to our footage of this species depredating a prothonotary warbler cavity during the egg stage, and a failed attack on an Acadian Flycatcher nestling that force-fledged from the nest, observation and circumstantial evidence supports the observation that red-bellied woodpeckers may have a substantial impact on nest survival in bottomland forests. During the 2006 field season, a red-bellied woodpecker was observed depredating a downy woodpecker (*Picoides pubescens*) cavity by excavating a small hole below the cavity entrance, at about the level of the cavity bottom. The red-bellied woodpecker then reached through the small opening, killed, dismembered, and extracted the chicks, in pieces, over several subsequent trips to the nest. A brief survey of old cavities throughout the forest confirmed that many of the old nest sites had similar small diameter openings at the base of the cavities. Though this evidence is only circumstantial, it suggests a specialized foraging strategy that may be used by this large woodpecker.

Brown-headed cowbirds were also observed depredating two nests. Their activities may be related to “farming” for host nests (i.e. the destruction of active nests to encourage renesting by hosts, which increases host availability) more than feeding opportunities (Arcese et al. 1996, Hoover and Robinson 2007). Regardless, their activities can contribute to reduced nest survival and, like the other predators noted above, may not always leave evidence of predation at a nest. This could result in over-estimation of nest-survival rates if nests lacking evidence of predation are counted as successful even though no fledglings are located (McCallum and Hannon 2001). In our case, we were conservative about concluding a nest successful, and returned to territories when we were uncertain about the fate of the nest, in an attempt to find fledglings with the parents. Use of continuous time-lapse video offers nest researchers the opportunity to assess the predator community influencing nest survival of their focal species, and to consider the likelihood of misclassifying depredations as successful fledge events as well as providing new insights about nest predators.

System related issues

Our in-house video monitoring system provides a relatively inexpensive (~$800.00) alternative to very expensive (e.g. $4,000/unit) units used in previous studies (Stake and Cimprich 2003). However, system failures resulted in substantial loss of data. Our study area provided some extreme conditions under which to test equipment, given the high humidity and heat during the summer breeding period. Self manufactured systems such as ours may be more subject to malfunction than professionally built systems engineered for rigorous field use. Thompson et al. (1999) and Stake and Cimprich (2003) experienced much lower failure rates with their commercial systems. The components we utilized in order to reduce expenses may be more likely to fail under high heat or humidity than more expensive materials. For this reason, researchers have to weigh the potential for failure or regular interruptions for maintenance against the need to capture every available datum. Studies of short duration where small sample size can limit the power of analysis might consider the potential for loss of data too great a risk, and opt for the stability and service options available from professional dealers.

Other researchers who have utilized homemade systems have had lower rates of failure in other study areas (Pietz and Granfors 2000; King et al. 2001; Sabine et al. 2005). This may relate either to the specific equipment used, or to the conditions under which it is used. In areas where heat and humidity are more moderate than the Mississippi Alluvial Valley, our system would likely work more smoothly. Even under the conditions faced there, we gathered valuable insights into the predator community. Researchers interested in behavior of nesting birds, or predators at the nest simply cannot rely on single image film or digital still cameras to provide adequate documentation (Purcell and Verner 1999).

The main technical issues (overheating, moisture, battery failure, wire damage) can be largely overcome by careful consideration of local weather conditions. Similar problems have been reported in other nest video studies using dissimilar systems (Thompson and Burhans 2003, Sabine et al. 2005, Pierce and Pobprasert 2007).

The decision regarding the choice of camera largely depends on the species being monitored, camera working distance (i.e. due to vegetation density), and what information is to be gathered. One area of concern has been the wavelength of the IR illumination provided standard with the camera or as accessories added by researchers. Studies using cameras with wavelengths similar to ours found no evidence that the lights influenced predation rates (Sabine et al. 2005). However, given the availability of 950-nm IR illuminating cameras, researchers should carefully consider what types of predators are expected and whether the shorter wavelength cameras may influence nest outcomes.

The availability of miniature cameras with variable focal lengths is also increasing. Some cameras, like the ones used in this study, allow lenses to be switched out, providing a specific level of magnification and fixed focal length, while some new cameras offer zoom lenses providing flexibility in the field. Older systems relied on cameras with extremely short working distances (i.e. 0.5 m) which were sometimes associated with nest abandonment (Stake and Cimprich 2003, Thompson and Burhans 2003). Our system allows much greater working distance and though a few nests were abandoned during filming, we did not feel that abandonment generally resulted from the nest camera's presence. Indeed, in several instances, female indigo buntings remained on the nest during camera deployment. This is remarkable because this species has been reported to react aversely to camera presence, sometimes abandoning the nest in earlier studies (Thompson and Burhans 2003).

One drawback of our specific VCR was the limited ranges of useful recording speeds. In several instances the four frame/second rate allowed a predator to depredate a nest and remain mostly or wholly unidentified. We chose this speed for several reasons. First, because it allowed 3 days of recording on a single T-120 VCR tape, which was just under the length of time a fully charged battery would last. Thus we reduced the cost associated with changing tapes and batteries at different or shorter intervals. The two faster settings would fill a tape in 36 and 24 hours. The 36 hour option offered nothing over the 24 hour option since tapes would have been removed before being full, and the 24 hour setting meant changing tapes every day, while changing batteries every three. Due to the distances involved between our field sites and cost associated with fuel and time, we felt this untenable.

Analog systems and, particularly the required power sources, tend to be bulky and heavy. The use of video tapes requires a great deal of space if substantial data are to be collected and archived. Digital systems are becoming available that offer a range of image capture rates and smaller, more efficient power sources (Pierce and Pobprasert 2007). Digital data can be saved onto compact disks and use very little space relative to the amount of data captured. Ongoing studies suggest that digital videography of songbird nests involves its own set of limitations and equipment issues, but like analog systems, these appear not to be insurmountable (A. Cox, *pers. comm.*).

Regardless of the type of system employed, videography is an important continuing step in the process of evaluating the range of factors influencing nest survival of passerine birds. For example, high canopy nests have long presented one of the more difficult to monitor groups, due to the difficulty of finding the nests initially, and of reaching them regularly afterwards. Assuming nests can be located via standard nest searching techniques (e.g. watching adult behavior), and given the substantial reduction in size possible with digital systems, advances in our knowledge of this nest guild is increasingly probable.

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