ILLINOIS NATURAL
HISTORY SURVEY
PRAIRIE RESEARCH INSTITUTE

The Effects of Bottomland Restoration on the Breeding Bird Community

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Duration of Research: May 1, 2011 to July 31, 2013

Prepared for: The Illinois Department of Natural Resources
State Wildlife Grant Program

Grant / Project Number: T-71-R-1
University Proposal Reference Number 2011-03429

INHS Technical Report 2013 (**)
Issue Date: TBD

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Project Title: The Effects of Bottomland Restoration on the Breeding Bird Community

Project Type: Site Inventories & Surveys, Research, and Measuring Success of Restoration

Project Period: May 1, 2011 to July 31, 2013

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Award Number: T-71-R-1 (U of I number 2011-03429; 595591)

Funding from: IDNR SWG: $40,000

Project Summary:

The Cache River Joint Venture Partnership (JVP; the Illinois Department of Natural Resources, The Nature Conservancy in Illinois, and the United States Fish and Wildlife Service) formed in 1991 in an effort to conserve and restore some 60,000 acres of bottomland forest habitat in the Cache River watershed of southern Illinois. During the past 19 years, the JVP has successfully acquired and re-forested over 20,000 acres of non-forested land. With the backing of the JVP, scientists from the Illinois Natural History Survey collected baseline data during 1993-1995 documenting breeding bird densities, breeding bird diversity, and nesting success of various species of bird prior to most of this land-use conversion. These conservation activities should result in increased nesting success and increased densities for many bottomland forest birds. We now have the unique opportunity to document how the restoration of bottomland forests (acquiring and "reforesting" non-forested land) has affected the diversity, abundance, and nesting success of Neotropical migratory birds breeding within a bottomland forest ecosystem.

This grant funded data collection during the multi-year project designed to meet several objectives including 1) determine the response of the breeding bird community to bottomland reforestation, 2) measure the success of the restoration efforts of conservation partners (IDNR, TNC, USFWS), and 3) provide results that are directly applicable to conservation plans and restoration efforts in other bottomland forest ecosystems.

This research represents the merging of scientific research with conservation in action and continues the partnership between the Illinois Natural History Survey (INHS) and the members of the Cache River JVP. The research proposed here will expand our knowledge and increase our ability to effectively and efficiently restore and manage bottomland forests. This research will ultimately provide guidelines to promote restoration and management practices that will provide the greatest benefit to Neotropical migratory birds residing in bottomland forest ecosystems, and will factor prominently in land conservation plans and land acquisition priorities. Also, the conservation issues being addressed and the results of this research have broad application and will assist with other bottomland forest restoration efforts in the Midwest and throughout the United States.

We include the project justification and objectives, and provide a summary of the highlights of what was accomplished during the project period. We are continuing to enter and analyze data from our bird surveys (point counts) and our nest searching and monitoring efforts (from both the period 1993-1995 and 2010-2012), and we will update IDNR with the results of new and additional analyses as we complete them. The size and scope of this database are such that we anticipate the publication of several manuscripts from it in the next 3 years and will send copies of those to IDNR as they become available.

Project Justification:

Neotropical migratory birds face continued threats resulting from the fragmentation and degradation of natural habitats. Research during the past 20 years has increased our understanding of the negative effects of habitat fragmentation (increased brood parasitism by cowbirds and increased nest predation) on migratory songbirds breeding in temperate bottomland forests, and land acquisition/conservation efforts that “unfragment” forests are possibly the best solution to restore or improve bottomland forest ecosystems.

In 1991, the Cache River JVP formed in an effort to conserve and restore (through land acquisition and reforestation) bottomland forest habitat in the Cache River watershed in Illinois. During 1993-1995, prior to most land acquisition and reforestation, we collected nesting data from seven focal sites within the Cache River watershed and obtained information on rates of nest predation and cowbird parasitism from nearly 2,000 nests (species include the Prothonotary Warbler, Kentucky Warbler, Louisiana Waterthrush, Acadian Flycatcher, Wood Thrush, Indigo Bunting, and Northern Cardinal). During that same period, we conducted point counts in >30 tracts of bottomland forest (at least 10 points per tract) throughout the watershed and documented bird abundance and diversity. Since then, over 20,000 acres of non-forested land have been acquired by the JVP and are in different stages of succession (1-20 years post-agriculture).

We have now completed the third year of a 3-year follow-up study to determine whether or not rates of nest predation and cowbird parasitism have decreased relative to the amount of restoration that has occurred. Point-count locations were revisited to determine the current abundance and diversity of breeding birds and to determine cowbird-to-host ratios (this ratio has been shown to be a good index of the community-wide rate of cowbird parasitism). This current data will allow us to compare changes in nesting success, bird abundance and bird diversity to changes in habitat configuration that are a direct result of the restoration efforts of the JVP. Data analyses are preliminary at this point, and there will be many additional results and publications that will be added to this report as they are completed.
The importance of the IDNR SWG to these efforts will be recognized in all publications resulting from this vast dataset and copies of these publications will be given to IDNR as they become available.

Too often the effects (i.e. success) of conservation/restoration efforts are not measured in terms of responses of the biota to the specific conservation actions. The research conducted here was designed to evaluate the success to date of conservation actions that should benefit birds breeding in bottomland forests. That evaluation will involve determining how changes in land-use in the Cache River watershed during the past 20 years, which are a direct result of land acquisition and restoration activities, affect bird diversity, bird densities, and nesting success. Therefore the success of this research and monitoring project will be measured in terms of our ability to have collected the necessary census and nesting data that will allow us to determine the benefits of bottomland forest restoration for these breeding birds. Results from this research will ultimately provide guidelines to promote restoration and management practices that will provide the greatest benefit to birds breeding in bottomland forest ecosystems. Also, the questions being addressed and the results of this research have broad application and will assist with other bottomland forest restoration efforts throughout the U.S.

Project Objectives:

By comparing current conditions to the preliminary data gathered during 1993-1995, we will:

1) Test the prediction that rates of nest predation and cowbird parasitism have decreased more in areas where there has been land acquisition and bottomland forest restoration than where there has been little restoration activity. This information will be critical to identifying where "source" habitats exist and will aid in prioritizing land acquisition.

2) Survey restoration plots that vary in age (e.g. 1-4, 5-9, 10-14, and 15-20 years post-agriculture) during **year 3** to document how the bird community changes in the restored areas (and the adjacent forest) as these agricultural fields transition to grassland, shrubland, and eventually to mature forest. This will provide important information to land managers at other sites who are managing for particular successional stages and their associated bird communities.

3) Use radio telemetry and genetic analyses to better understand how cowbirds use the landscape in the Cache River watershed, to document daily patterns of habitat use and parasitism activities of adult female cowbirds, and to gain a better understanding of how long juvenile cowbirds remain with their host parents and the process by which they disperse away from the forest to join other cowbirds.

4) Determine the effects and success of restoration efforts in the Cache River watershed to date, and provide information critical to the continued conservation efforts of the JVP and other bottomland forest restoration projects throughout the U.S. This completed research will result in several peer-reviewed manuscripts that will provide information that will further the science of restoration ecology and be useful to both local and regional ecosystem management efforts.

Cache River Bird Research Summary

The most important breeding bird data collected from the Cache River watershed during the past 3 years is that associated with the finding and monitoring of bird nests to document rates of nest predation and cowbird parasitism, to determine how successfully birds are able to breed in the Cache River watershed, and to compare this nesting success to that of birds nesting on the same study sites in the early 1990s prior to the bulk of the land acquisition and reforestation that has taken place during the past 20 years. These data are costly and time consuming to collect but provide the best direct test of whether conditions for breeding birds have improved as a result of all of the reforestation efforts accomplished by the JVP. Collectively, the 1,000 nests of various species found during 2010-2012 along with the 1,200 found during 1993-1995 will be plotted in a GIS program and we are working to estimate habitat characteristics (e.g. distance to edge, edge density, forest cover within varying distances) for analyses of the effects of changes in land-use configuration (in association with restoration) on rates of nest predation and cowbird parasitism.

Cowbird Parasitism: Qualitatively, the pattern documented during 2010-2011 of relatively low rates of cowbird parasitism in those study sites surrounded by mostly restored (i.e. reforested) land remained consistent through 2012 supporting the conclusion that reforestation in the Cache has significantly reduced the problem of cowbird parasitism. These results are a shining example of how "unfragmenting" forests within a floodplain can have the predicted effect of reducing rates of cowbird parasitism for several species of migratory songbird that serve as hosts to cowbirds. Cowbird parasitism has dropped markedly in the study sites since the period 1993-1995 (see Figs. 1 and 2). For Acadian Flycatchers, the species with the most nesting data, overall rates of cowbird parasitism are now half what they were (**38%**

during 1993-1995 vs. 19% during 2010-2012; Fig. 1). Averaging across the other 6 species of hosts we have data for, overall rates of cowbird parasitism are less than half what they once were (**53% during 1993-1995 vs. 22% during 2010-2012**; Fig. 2) The likely reasons for this decrease in cowbird parasitism in association with bottomland forest restoration (acquiring agricultural land and converting in back to bottomland forest) include the potential for 1) the restoration to increase the commuting distance of female cowbirds that now have to fly farther away from their forest breeding areas to find suitable feeding areas and 2) the absorbing of some cowbird eggs by the many cowbird hosts now occupying the early successional stages of restored bottomlands adjacent to the original mature bottomland forest (see "birds associated with forest successional stages" section below).

Nest Predation: A preliminary assessment of the data used to determine rates of nest predation for Acadian Flycatchers and the other 6 main species monitored was also completed. The overall rate of nest predation for Acadian Flycatchers was 7% lower during 2010-2012 (51%) compared to 1993-1995 (58%) and was lower on 3 of 5 study sites (Fig. 3). The overall rate of nest predation for the other 6 species (averaged across species) was 12% lower during 2010-2012 (52%) compared to 1993-1995 (64%) and was lower on 4 of 5 study sites (Fig. 4). Similar to, but not as dramatic as, the result with cowbird parasitism, these changes are likely a result of land acquisition and reforestation that has occurred to more and less of an extent in proximity to the various study sites. We are aware that there are several types of nest predators in bottomland forests including a variety of mammals, birds, and snakes, and each predator may respond differently to the land conversion occuring in the Cache River watershed. That rates of nest predation overall are tending to be lower is promising and suggests that the decrease in the amount of agricultural matrix and "edge" habitat in the watershed may be playing a role. Our goal is to now determine quantitatively how the changes in landuse that have occurred between the early period (1993-1995) and the present have affected the rates of both nest predation and cowbird parasitism.

Birds Associated with Forest Successional Stages: The presence and abundance of birds in 5 categories (agriculture and 4 successional stages; 1-4, 5-9, 10-14, and 15-20 years after agriculture transitioning into bottomland forest) followed a predictable trajectory. There were relatively few bird species present in corn and soybean fields, and then bird diversity increased dramatically and topped out in the categories of 5-9 and 10-14 years after agriculture before decreasing somewhat as the shrubland became a young forest (Fig. 5). It is typical for the shrubland bird community to be more diverse than that of birds breeding in young forests. Usually by the time the bottomland forest reaches 30-40 years of age, the bird diversity starts to increase again (as more forest bird species move in) and should surpass the bird diversity seen in the shrubland habitat as the forest matures beyond 40 years of age (often > 60 species breeding in mature forests). The composition of the birds breeding in the categories of succession changed quite dramatically as the agricultural field reverted back to grassland, shrubland and eventually to young forest habitat (Figs. 6-7). Figures 8-12 highlight the abundance of each individual species that was detected in any of the surveys conducted, and these figures are grouped by general categories that include birds associated most with agriculture (Fig. 8), grassland (Fig. 9), early shrubland (Fig. 10), late shrubland (Fig. 11), and young forest (Fig. 12).

One of many highlights of this data was the relatively high abundance of some conservation priority species (shrubland birds) in the 5-9 and 10-14 years after agriculture categories including Bell's Vireo, Yellow-breasted Chat, Brown Thrasher, Gray Catbird and Prairie Warbler. Another interesting and important result was that the Brown-headed Cowbirds were present in 4 of the 5 categories. In the agriculture, they were present because they were foraging on the ground in the soybean and corn fields. In the other categories, they were present because they were looking for nests (of hosts) to parasitize. Where there once was agriculture adjacent to our mature forest study sites, there is now a lot of land that is at various successional stages reverting to forest. It is very likely that the relatively rich host communities present in this successional habitat (following the acquisition and conversion of agricultural land) now adjacent to our mature forest study sites is absorbing some of the cowbird parasitism that would have otherwise been in the mature forest. This provides one possible explanation for why the rates of cowbird parasitism have dropped in the mature forest sites over time (comparing the 1993-1995 period with the 2010-2012 period; Figs. 1-2), particularly for those forests that now have a lot of successional habitat surrounding them compared to the early 1990s.

Cowbird Telemetry and Genetics: *Telemetry 2011*: Radio transmitters (1.4 g) were attached to 5 adult Brown-headed Cowbird females captured within putative breeding areas, located in two forested wetlands (Hickory Bottoms in the Cypress Creek NWR and Main Tract in the Cache River SNA). Each female was observed 1 to 5 times a week throughout the life of the transmitter (~ 10 weeks). During the morning hours, each individual female cowbird was predictably located within their respective forest "territories" (~ 6 ha in size) in the vicinity of their initial capture location. Females departed the forested wetlands at variable times during the afternoon hours (~2-5 pm). When located out of the forest, females were typically found foraging within agriculture fields and grass lawns adjacent to houses (0.5 – 1.5 km from their respective breeding territories in the forest). Most females observed in agriculture were found foraging in unplanted fields and recently planted soybeans. However, as the water levels dropped within the swamps during late June and early July, females were occasionally observed foraging on the exposed mudflats of drained swamps within the forest near their respective breeding areas.

We placed transmitters (0.9 g) on 10 juvenile cowbirds prior to fledging from Prothonotary Warbler nestboxes (early June - early July). We attempted to detect any interaction between adult female cowbirds and juvenile cowbirds by attaching transmitters on juvenile cowbirds that fledged from a nestbox located within the "territory" of a radio-tracked adult female cowbird. Of the 10 juveniles, 5 were preyed upon within the first two days after fledging and 1 died of unknown causes 2 weeks after fledging. Juveniles became independent from their host (warbler) parents 20-25 days after fledging (n = 4). Each juvenile found after dispersing (n = 3), was located in small cowbird flocks foraging in grass lawns (n = 2) or recently planted soybean (n = 1). Juveniles dispersed 0.5-0.8 km from their respective nestboxes. We failed to locate one juvenile after it apparently dispersed form the forest. Although adult females were often observed within close proximity of juvenile cowbird fledglings, it remains unclear if female cowbirds lead juvenile cowbirds out of the forest to foraging areas.

Telemetry 2012: Radio transmitters (1.4 g) were attached to 8 adult Brown-headed Cowbird females captured within breeding areas in two forested swamps within Cypress Creek NWR. One female was known to have fledged from a Prothonotary Warbler nestbox 150m away in the previous year indicating that cowbirds can return as adults to parasitize the very host that served as their foster parent in the previous year. During the morning hours, each individual female cowbird was predictably located within their respective forest "territories" (~ 6.5 ha) near their initial capture location. Females departed the forested swamps at variable times during the afternoon hours (~2-5 pm). When located, females were typically found foraging within agriculture fields, grass lawns adjacent to houses and two different cattle pastures (0.5 – 1.5 km from respective territories). Female cowbirds did not necessarily follow a simple "forest in the morning and pasture in the afternoon" schedule. Many of the female cowbirds, particularly if their forest breeding area was close to a suitable feeding area, would commute back and forth several times daily over the course of the entire day.

In 2012 we also attached transmitters (0.9 g) to 13 juvenile cowbirds prior to fledging from Prothonotary Warbler nestboxes (late May - early July). Only 4 of the 13 juveniles (30%) survived to independence from the host. Juveniles were typically preyed on within the first 2 days after fledging, and if they survived past those two days, became independent from their host parents 20-25 days later. Juvenile survival both before and after fledging was lower in 2012 compared to 2011. The extreme drought conditions appeared to have decreased the food supply as many nestling songbirds died at various stages throughout the nesting cycle. Many nestboxes were also preyed on by large avian predators. These same predators may have been responsible for the increased predation rates during the post-fledging period.

The Automated Radio Telemetry System (ARTS) was successful in detecting the presence/absence of both adult female cowbirds and juveniles within the main study site (Hickory Bottoms). Detailed activity patterns revealed interesting patterns for both adults and juvenile cowbirds. On numerous occasions, female cowbirds were detected flying near the site, and occasionally within the site between midnight and 4 am. As the juvenile cowbirds neared independence from the host, each juvenile was detected leaving their respective host parents and forest patch just before dusk, only to return to the care of the host the following morning. This behavior was carried out for over 5 days for each individual. Although the reason for this behavior is currently unclear, it likely plays a role in the development of juvenile cowbirds and may aid in their ability to disperse from their host and ultimately find and join cowbird flocks. Without the ARTS system, it is unlikely we would have been able to document the nocturnal patterns observed for either the juvenile or adult cowbirds.

Cowbird Genetics: Female Brown-headed Cowbirds tend to be cryptic in forested habitat while searching for hosts to parasitize. Therefore, traditional methods of catching and re-sighting individuals in the habitats cowbirds use has limited utility in understanding how many individuals are present in a particular habitat patch, how large their home ranges are, and how many and which types of hosts individuals female cowbirds are using. In the past several decades, microsatellite markers have been developed for brown-headed cowbirds to help elucidate these behaviors. We took DNA samples from brown-headed cowbird adults ranging in particular forest patches, cowbird juveniles being raised by various hosts, and from cowbird eggs/embryos from known hosts (primarily Prothonotary Warblers) throughout the Cache Watershed in southern Illinois in order to determine how many female cowbirds occupy forest patches of different sizes and in varying proximity to restoration. With these data, we will be able to 1) identify the mothers of juvenile and egg/embryo cowbirds if the adult female was genetically sampled; 2) reconstruct sibling groups in forest patches and reconstruct maternal genotypes if they have not been sampled; and 3) determine whether the same female cowbird was responsible for cases of multiple parasitism in a single nest. In the end, through genetic analyses, we will have a good estimate of the number of female cowbirds operating in a particular forest patch, we will know their approximate egg-laying range and whether multiple females overlap in those ranges, and we will know whether multiple parasitism events (more than one cowbird egg in a single nest) are from the same or different females. We should also be able to use the genetic data to determine whether particular female cowbirds are present across several years and whether any of the cowbird offspring produced return close to their natal area.

DNA was extracted from all blood samples using Qiagen® DNeasy tissue kits (Qiagen Inc., Valencia, CA, USA). We identified nine microsatellite loci by screening published primer sequences from Brown-headed Cowbirds (Table 1). We optimized primers for ideal PCR conditions. Forward primers were labeled with either FAM, NED or HEX 5'-flourescent labels for genotyping. PCR reactions were performed in 12-tube strips using a Bio-Rad® thermal cycler. Each 15-µl reaction contained at least 50 ng genomic DNA, 0.24 µM of each primer, 800 µM dNTPs, 1x PCR buffer, 0.5 U of *Taq* polymerase (5Prime, Hauppauge, NY, USA), and a primer-specific $MgCl_2$ concentration (0.5 to 2.5 mM). Fragment sizes for all PCR products were analyzed by the Keck Biotechnology Core Lab at the University of Illinois using an ABI 3730 (Applied Biosystems Inc., Foster City, CA, USA). Fragment data were sized and scored using using GENEMAPPER software (Applied Biosystems Inc.).

We collected over 3000 DNA samples from cowbirds throughout the study. Each primer was tested on a set of adult and juvenile brown-headed cowbirds from the Cache Watershed (n = 126) sampled from 2009 through 2012 to assess allelic diversity, test for Hardy-Weinberg equilibrium, the frequency of null alleles and linkage disequilibrium. Allelic diversity ranged from 6 to 28 alleles (Table 1) and no locus deviated significantly from Hardy-Weinberg equilibrium nor did any loci show evidence of linkage disequilibrium. The frequency of null alleles ranged from 0.01 to 0.16, with the majority of loci having a low frequency of nulls (< 0.05). The one exception was Mau20, which had a high frequency of nulls and will not be useful in maternity analyses. Preliminary results from the identified markers indicate that we have good statistical power to identify the mothers of cowbird offspring (Table 1, combined P_{first_parent} exclusion probability = 0.9995). Genotyping is currently underway and will be completed by May 2014. Once all of the genotypes are compiled, we will be able to begin analyses on female ranging and laying behavior in the Cache River Watershed.

Table 1. Summary statistics of nine microsatellite loci that will be used to determine maternity in brown-headed cowbirds; n, number of individuals genotyped; NA, number of alleles; H_O, observed heterozygosity; H_E, expected heterozygosity, P_{First_Parent}, probability of first-parent exclusion, P_{Second_Parent}, probability of second parent exclusion with a known first parent

Locus	n	Na	Allele size range	Het_o	Het_E	P_{first_parent}	P_{second_parent}	Estimated frequency of null alleles
CB12	126	28	188-256	0.992	0.912	0.309	0.183	-0.0461
CB15	126	16	238-324	0.897	0.898	0.351	0.212	-0.0022
MAU10	126	8	158-174	0.691	0.653	0.751	0.573	-0.0315
MAU20	126	11	121-157	0.635	0.887	0.384	0.236	+0.1604
MAU25	126	26	117-177	0.905	0.933	0.251	0.144	+0.0132
MAU29	126	20	128-174	0.952	0.862	0.462	0.274	-0.0555
MAU101	126	18	141-189	0.810	0.830	0.500	0.331	+0.0106
MAU102	126	6	167-179	0.397	0.412	0.908	0.757	+0.0269
MAU104	126	16	137-176	0.865	0.896	0.356	0.216	+0.0156
					Combined Exclusion Probability	0.9995	0.9999	

<u>The flood of 2011</u>: The record flood of 2011 delayed by 2-3 weeks the nesting of many species (particularly Prothonotary Warblers and Kentucky Warblers) in the bottomland forests of the Cache River watershed. Once the flood waters receded, the Prothonotary Warblers quickly began nesting and by mid-summer had reached densities similar to previous years. Favorable nesting conditions for the warblers (i.e. deep water beneath nests keeping away predators [raccoons] and abundant food [insects]) extended into early August (2 weeks later than usual) leading to overall reproductive output similar to previous years. The habitat of species nesting on or near the ground (e.g. Kentucky Warblers) was inundated and subsequently so altered that only in late June and July were there any Kentucky Warbler nests built in the floodplain forests of the Cache. In this regard, there was only a small percentage (e.g. 10-15%) of the typical number of pairs of Kentucky Warblers nesting in the floodplain forests. While the short-term effects of the flood on Kentucky Warblers were negative, the scouring of vast areas of the understory should lead to excellent nesting habitat (dense ground cover) for Kentucky Warblers during subsequent breeding seasons.

The Drought of 2012: We conducted an initial assessment of the 2012 Prothonotary Warbler data to determine if there was an effect of the 2012 drought on productivity (number of warblers fledged from nest boxes) in this species. We compiled data from 12 study sites, each monitored similarly during 2010-2012. We compared the average productivity of 2010-2011 to that of 2012 for each site. Across all 12 study sites, we found that the number of warblers fledged in 2012 was on average **32% lower** than in the previous two years (2010-2011). Productivity of the warblers was lower in 2012 on **all 12** study sites (range = 9% to 73% lower). We are now trying to determine how the drought caused this decline (e.g. increased nestling starvation, reduced renesting by females, shortened breeding season, food limitation, a combination of these things, etc.).

We are now working towards mining the rich breeding bird database from the Cache River watershed with the goal of publishing several manuscripts. To reiterate, the Illinois Department of Natural Resources will be acknowledged for their important role in this research in any and all publications that result, and we will send copies of all manuscripts to IDNR when they are published.

Some of the data collected during the course of this grant were used in the completion of 2 Master’s theses (one thesis is attached to the end of this report, and a paper published from the other thesis is also attached). The abstracts of each provide the essence of the results, and the details are given in the bodies of the thesis and manuscript, respectively.

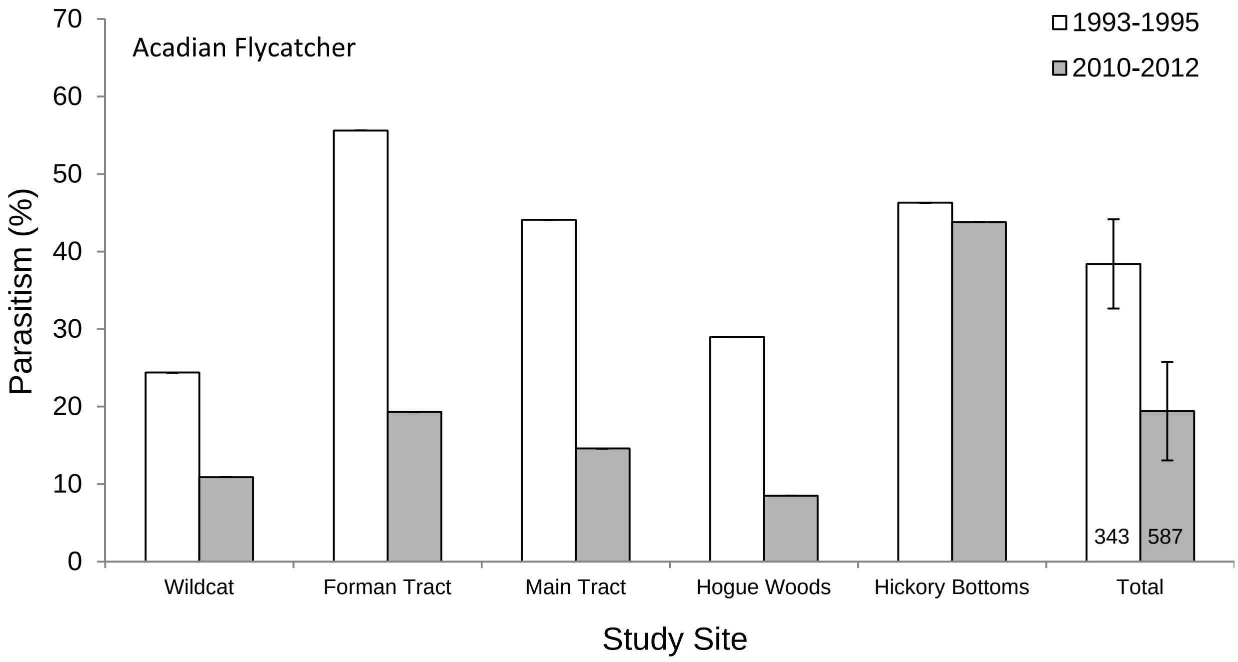

Figure 1. Rates of cowbird parasitism for Acadian Flycatchers nesting in the Cache River watershed during 1993-1995 and 2010-2012. Rates for each site are averaged across years. Values for total nests within each time period (±1SE) are averaged across sites. Total number of nests during each time period given inside of bars in the “Total” category. Hickory Bottoms site has had the least reforestation adjacent to it.

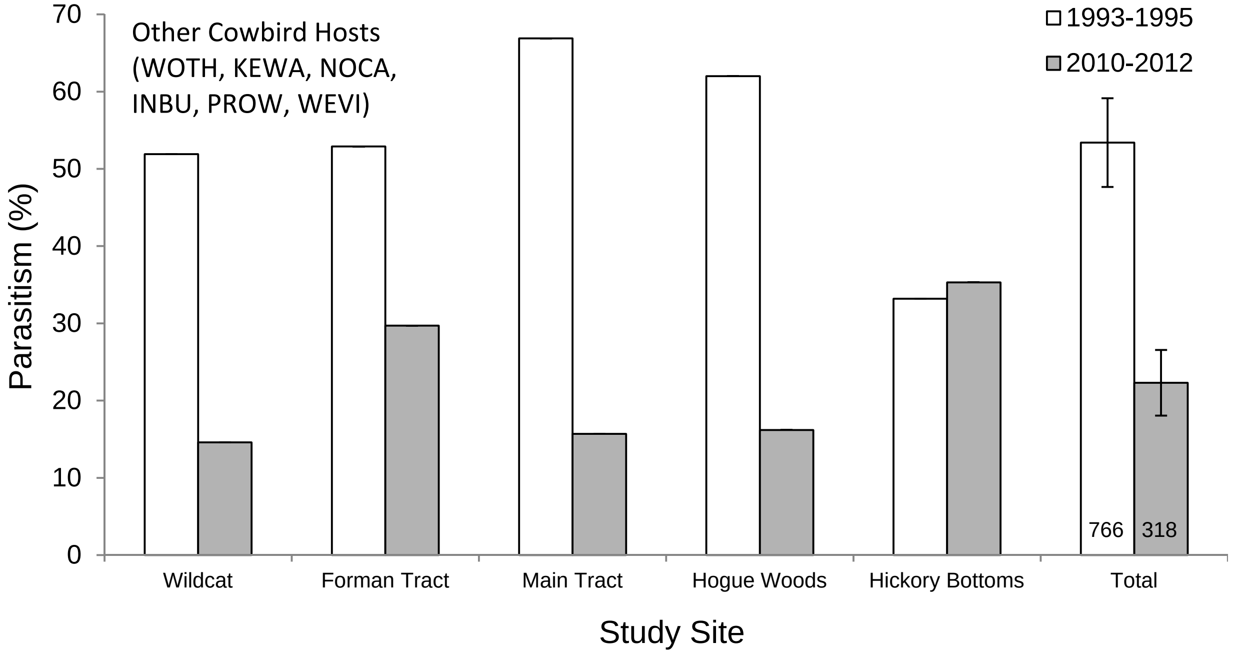

Figure 2. Rates of cowbird parasitism for other cowbird hosts nesting in the Cache River watershed during 1993-1995 and 2010-2012. Other hosts include Wood Thrush, Kentucky Warbler, Northern Cardinal, Indigo Bunting, Prothonotary Warbler, and White-eyed Vireo. Rates for each site are averaged across years. Values for total nests within each time period (±1SE) are averaged across sites. Total number of nests during each time period given inside of bars in the "Total" category. Hickory Bottoms site has had the least reforestation adjacent to it.

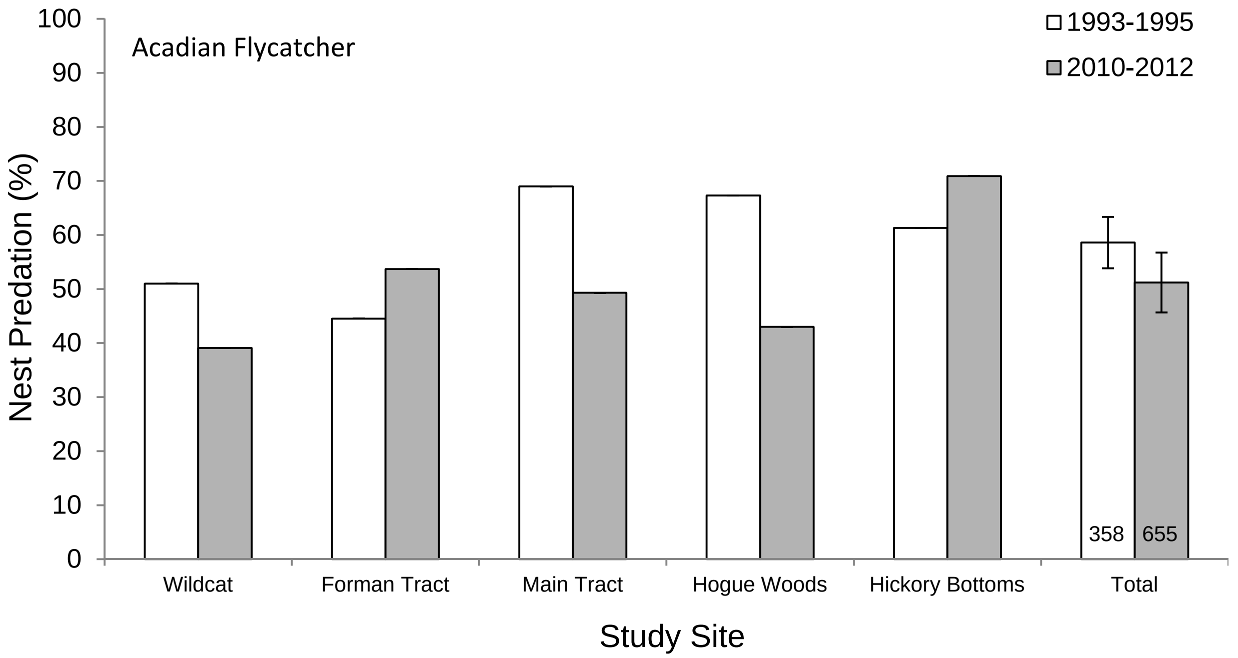

Figure 3. Rates of nest predation for Acadian Flycatchers nesting in the Cache River watershed during 1993-1995 and 2010-2012. Rates for each site are averaged across years. Values for total nests within each time period (±1SE) are averaged across sites. Total number of nests during each time period given inside of bars in the "Total" category. Hickory Bottoms site has had the least reforestation adjacent to it.

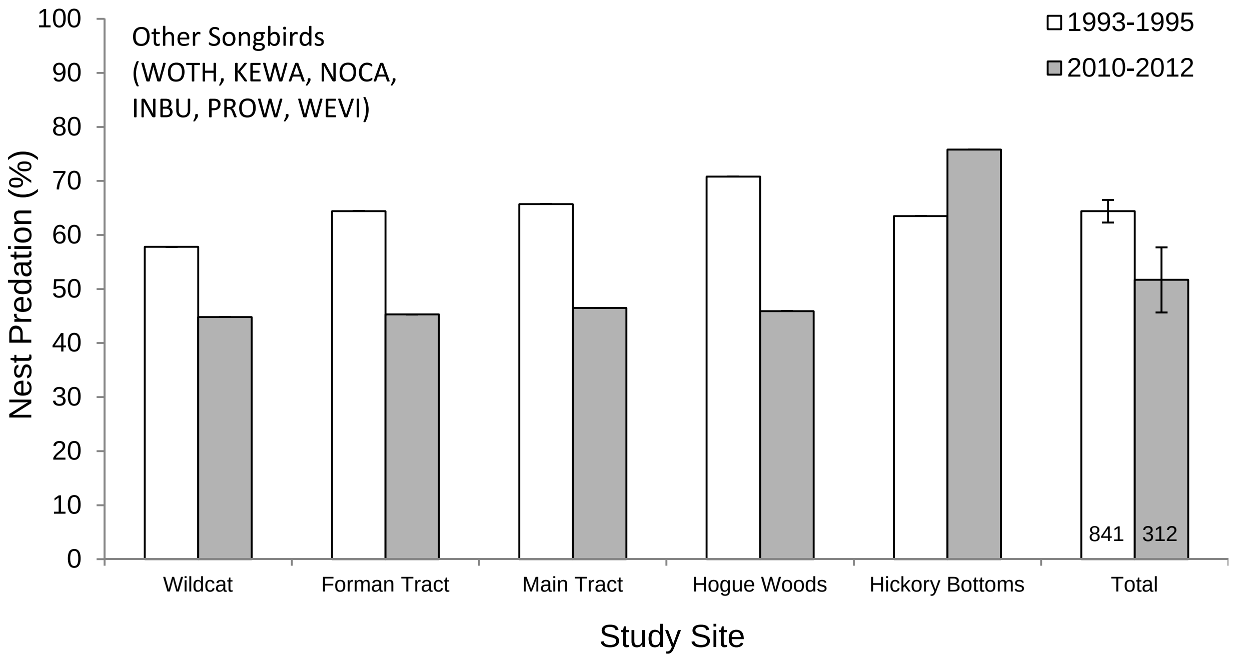

Figure 4. Rates of nest predation for other songbirds nesting in the Cache River watershed during 1993-1995 and 2010-2012. Other songbirds include Wood Thrush, Kentucky Warbler, Northern Cardinal, Indigo Bunting, Prothonotary Warbler, and White-eyed Vireo. Rates for each site are averaged across years. Values for total nests within each time period (±1SE) are averaged across sites. Total number of nests during each time period given inside of bars in the “Total” category. Hickory Bottoms site has had the least reforestation adjacent to it.

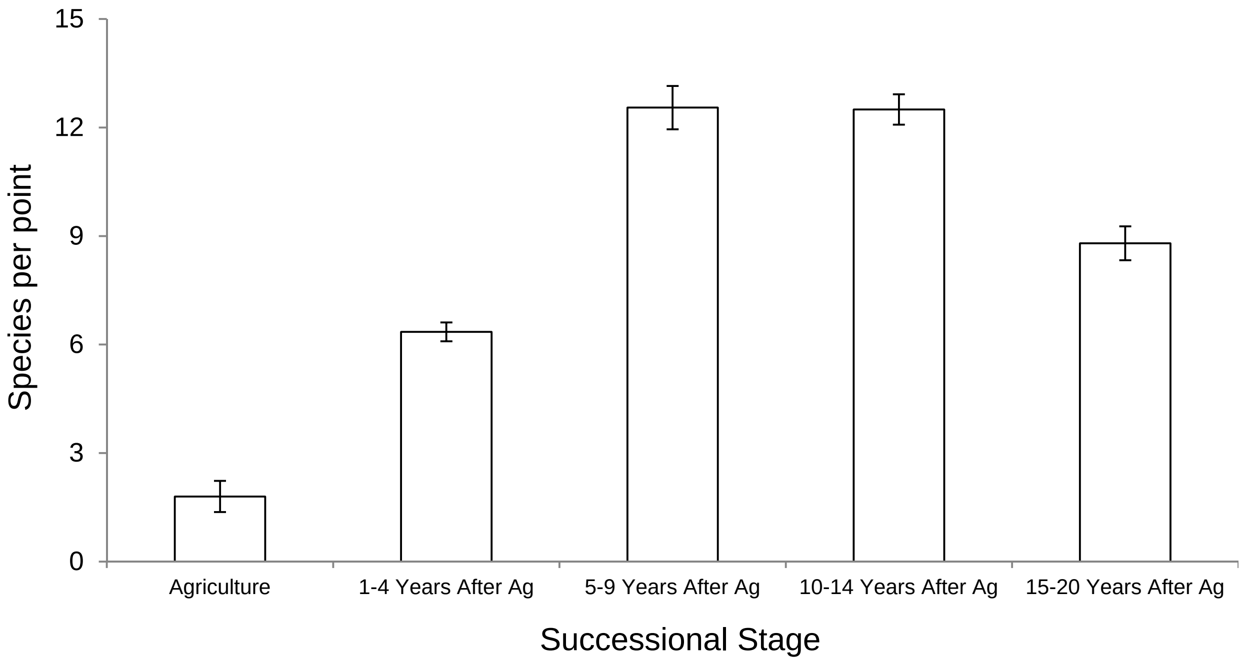

Figure 5. A measure of breeding bird diversity (mean species ±1SE per survey point) compared among 5 categories across a forest succession gradient. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each category during 2012 in the Cache River Watershed.

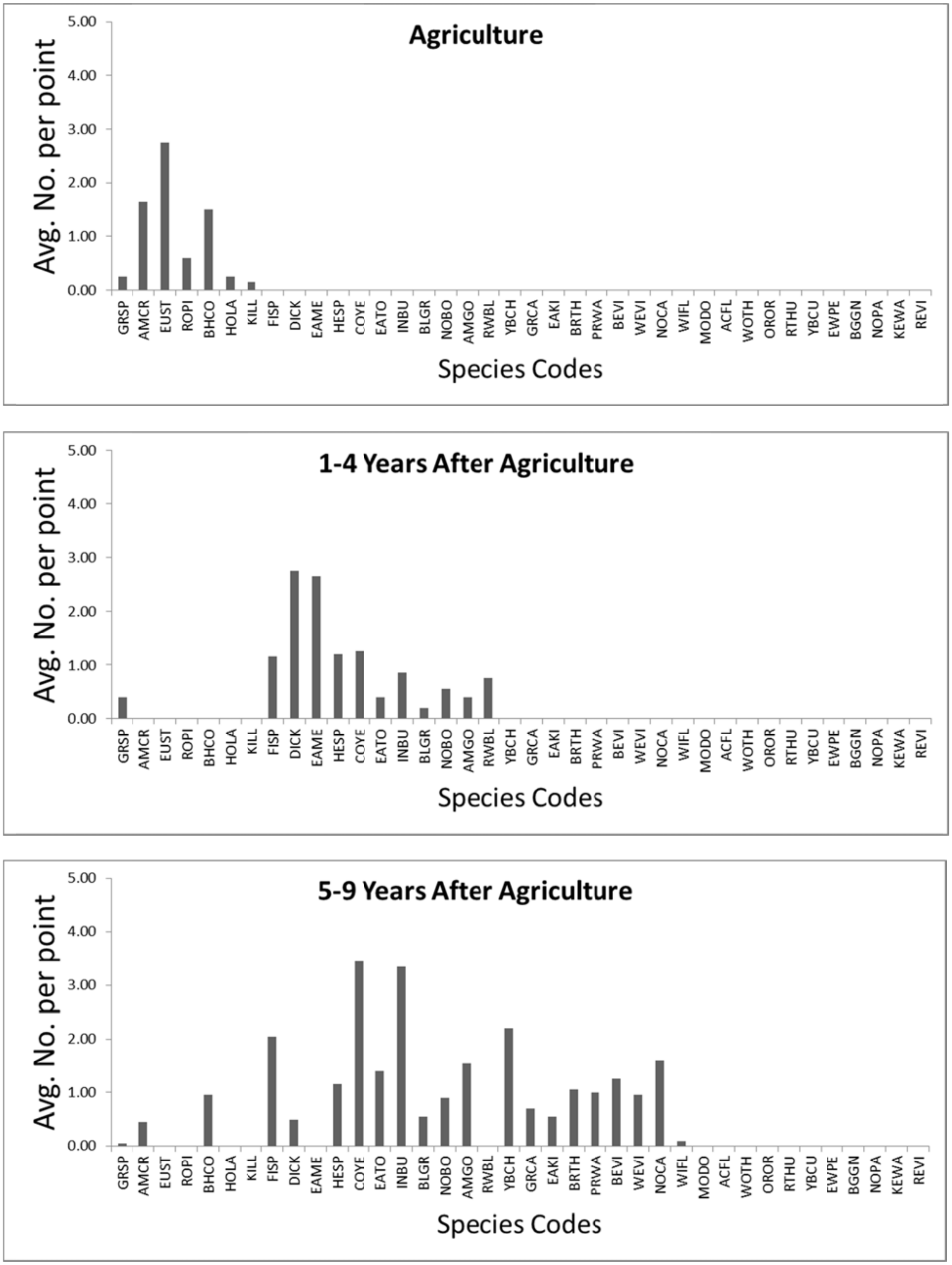

Figure 6. Abundance of species in different successional stages following acquisition of agricultural land and reversion to forest. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed. Species codes listed in Figure 7 legend.

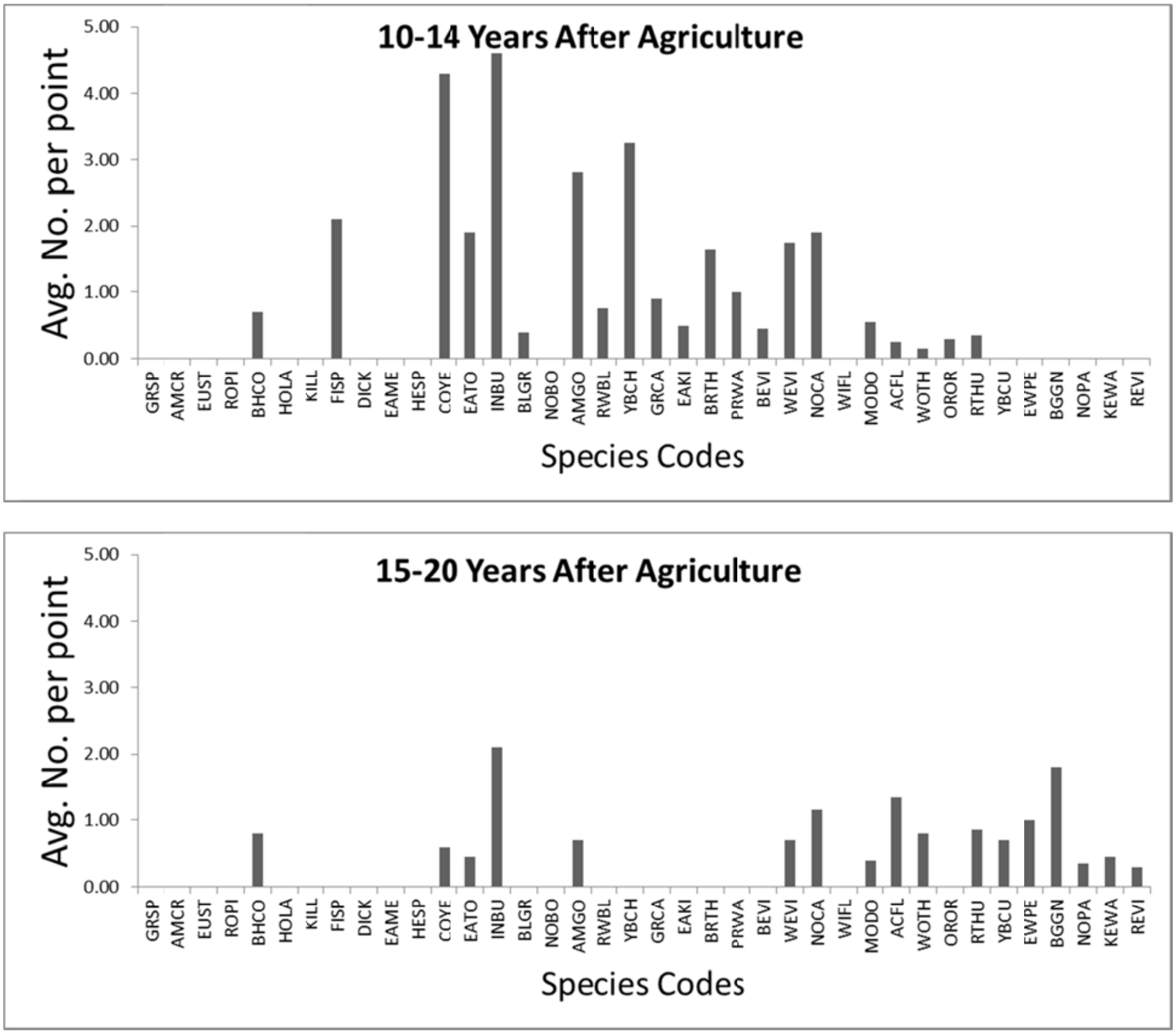

Figure 7. Abundance of species in different successional stages following acquisition of agricultural land and reversion to forest. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed. Species codes: GRSP=Grasshopper Sparrow; AMCR=American Crow; EUST=European Starling; ROPI=Rock Pigeon; BHCO=Brown-headed Cowbird; HOLA=Horned Lark; KILL=Killdeer; FISP=Field Sparrow; DICK=Dickcissel; EAME=Eastern Meadowlark; HESP=Henslow's Sparrow; COYE=Common Yellowthroat; EATO=Eastern Towhee; INBU=Indigo Bunting; BLGR=Blue Grosbeak; NOBO=Northern Bobwhite; AMGO=American Goldfinch; RWBL=Red-winged Blackbird; YBCH=Yellow-breasted Chat; GRCA=Gray Catbird; EAKI=Eastern Kingbird; BRTH=Brown Thrasher; PRWA=Prairie Warbler; BEVI=Bell's Vireo; WEVI=White-eyed Vireo; NOCA=Northern Cardinal; WIFL=Willow Flycatcher; MODO=Mourning Dove; ACFL=Acadian Flycatcher; WOTH=Wood Thrush; OROR=Orchard Oriole; RTHU=Ruby-throated Hummingbird; YBCU=Yellow-billed Cuckoo; EWPE=Eastern Wood-pewee; BGGN=Blue-gray Gnatcatcher; NOPA=Northern Parula; KEWA=Kentucky Warbler; REVI=Red-eyed Vireo.

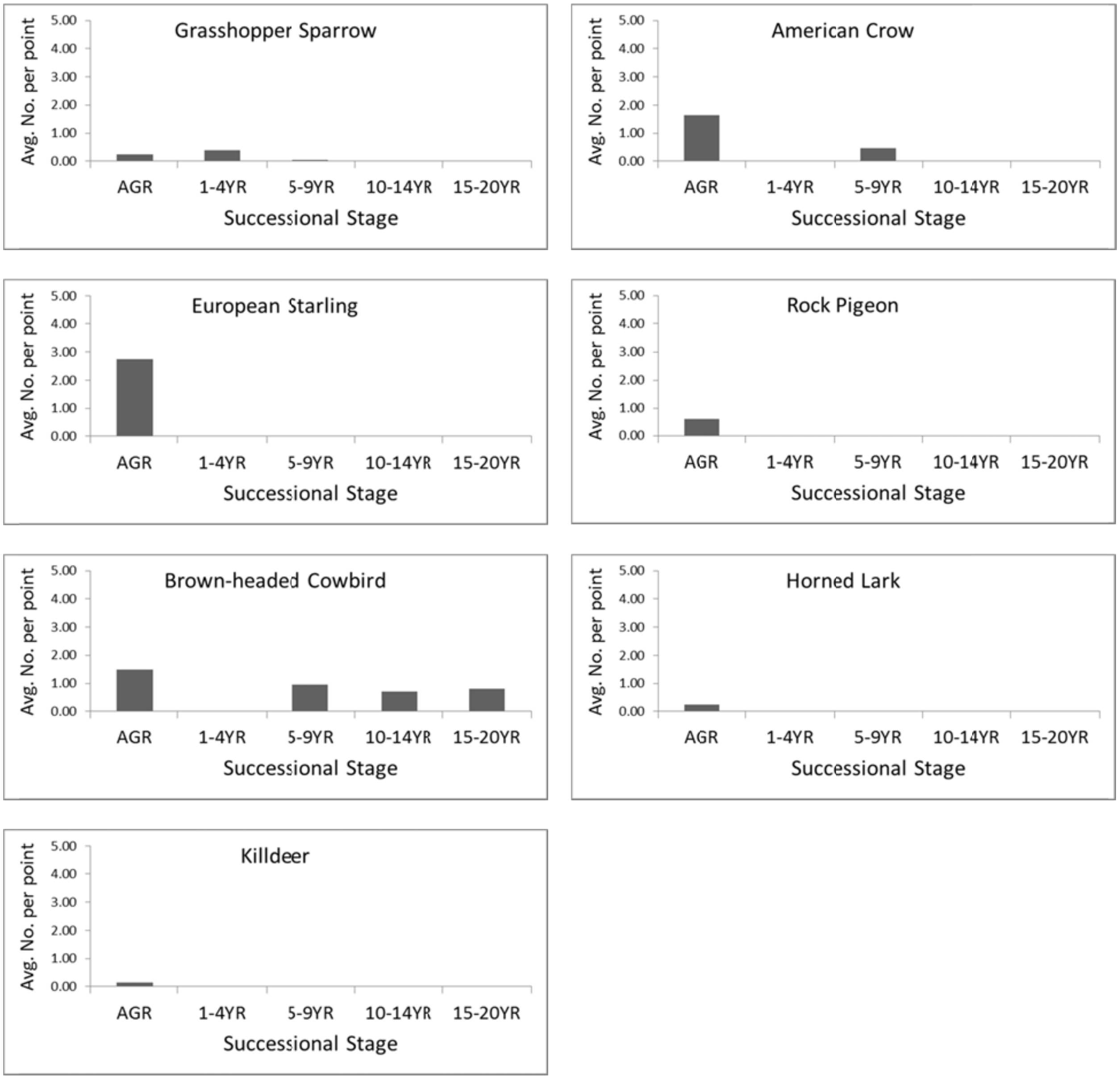

Figure 8. Abundance of individual species in different successional stages following acquisition of agricultural land and reversion to forest. Species above were found primarily in Agriculture. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed.

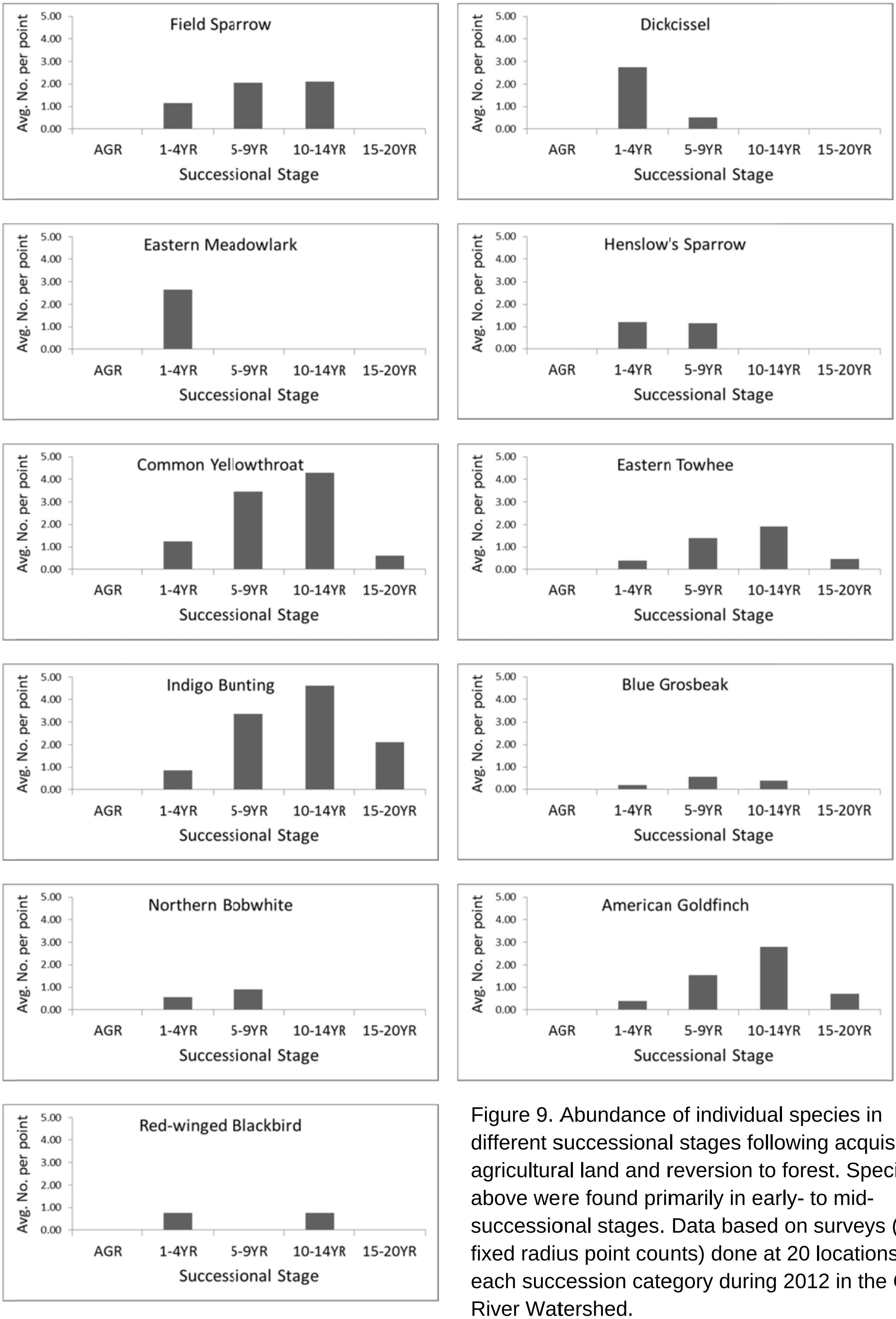

Figure 9. Abundance of individual species in different successional stages following acquisition of agricultural land and reversion to forest. Species above were found primarily in early- to mid-successional stages. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed.

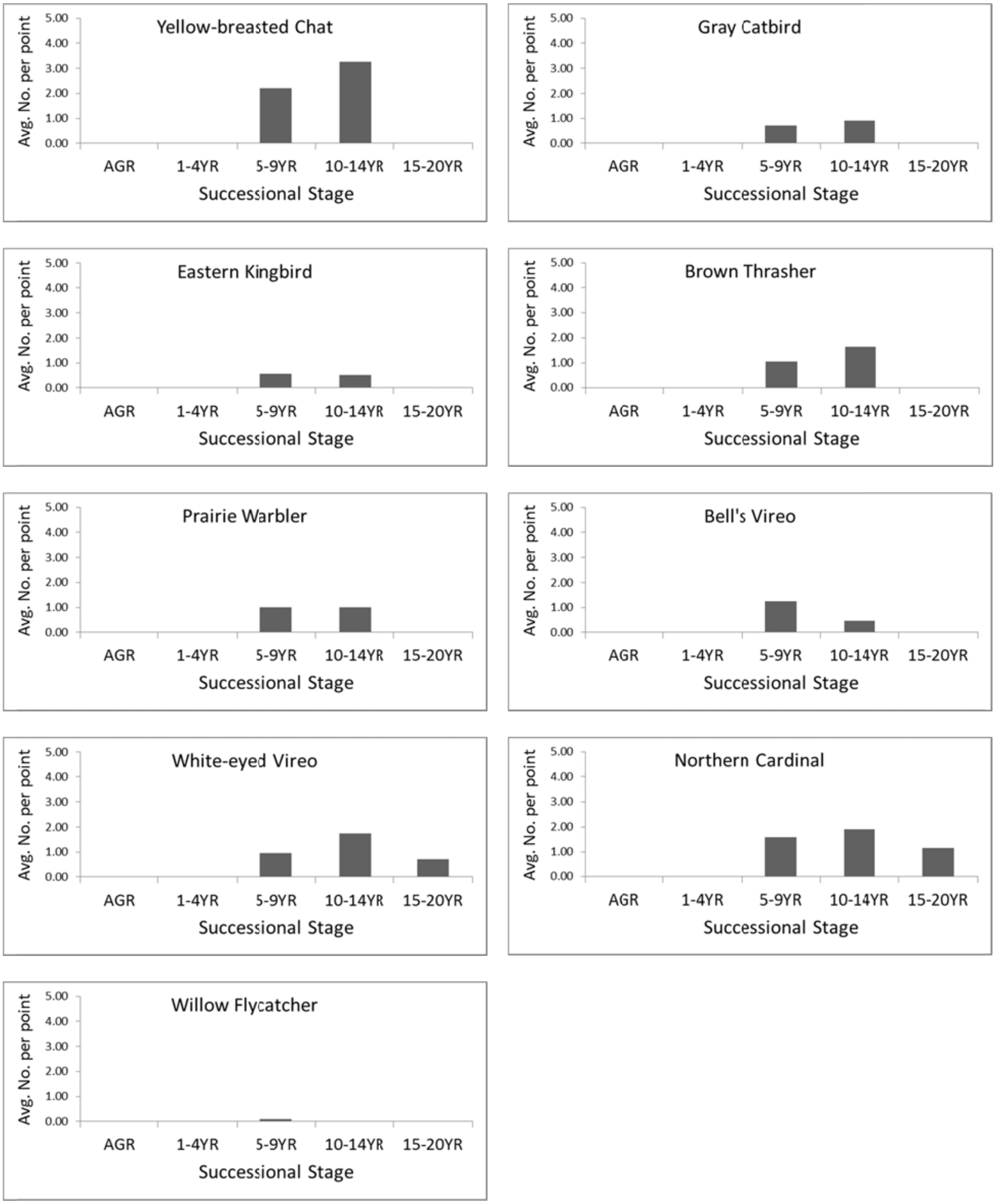

Figure 10. Abundance of individual species in different successional stages following acquisition of agricultural land and reversion to forest. Species above were found primarily in mid-successional stages. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed.

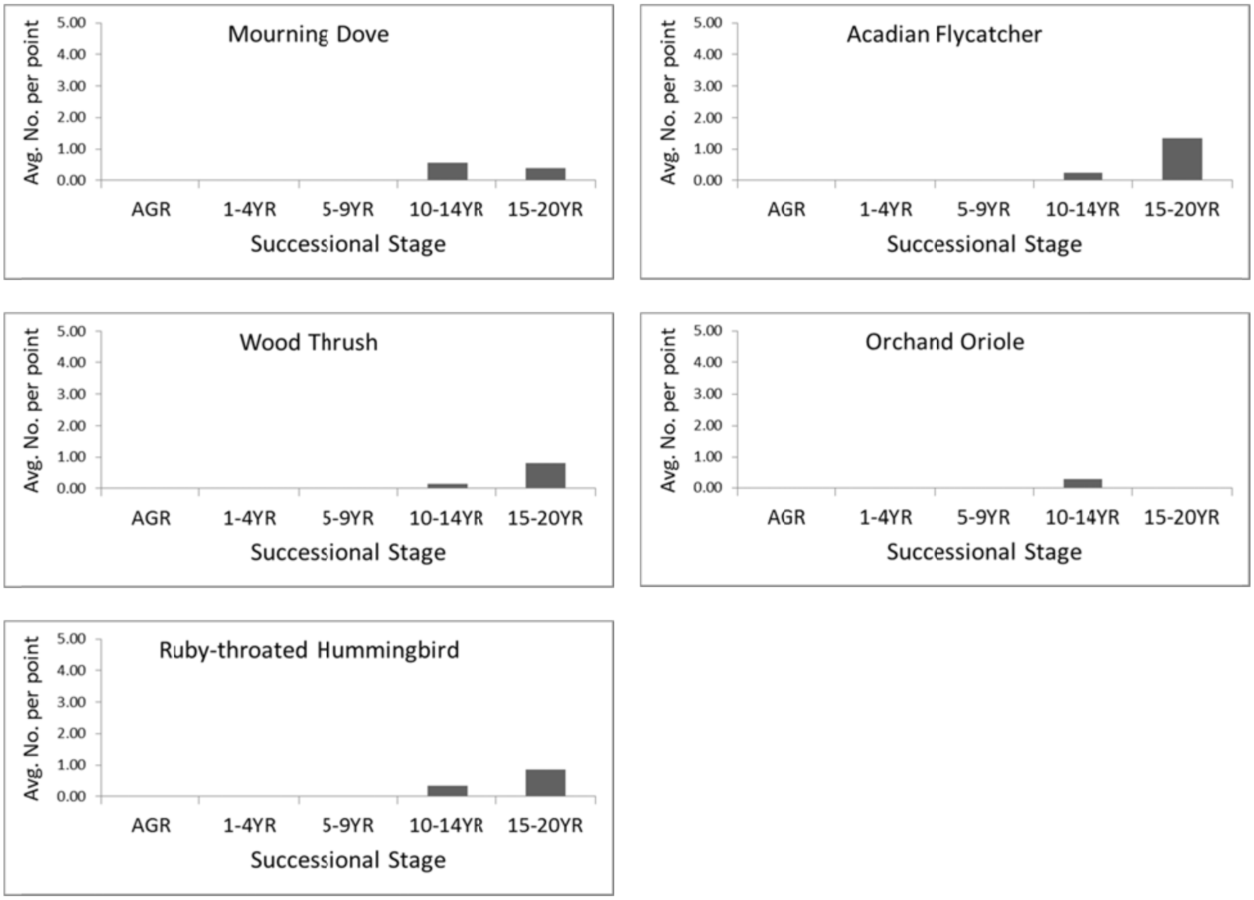

Figure 11. Abundance of individual species in different successional stages following acquisition of agricultural land and reversion to forest. Species above were found primarily in mid- to late-successional stages. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed.

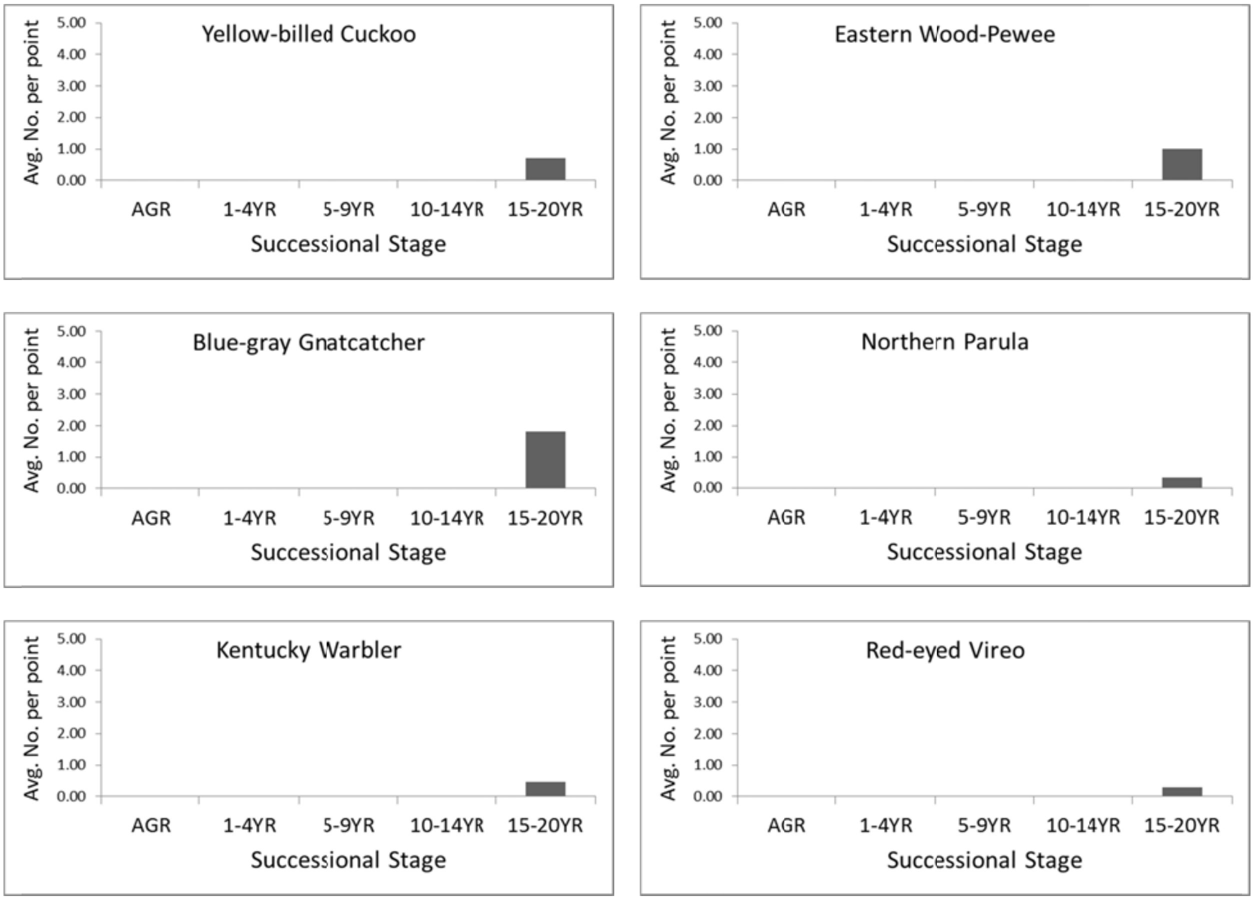

Figure 12. Abundance of individual species in different successional stages following acquisition of agricultural land and reversion to forest. Species above were found primarily in the late-successional stage. Data based on surveys (100-m fixed radius point counts) done at 20 locations in each succession category during 2012 in the Cache River Watershed.

REPRODUCTIVE SUCCESS OF A GENERALIST BROOD PARASITE PREDICTS THE RATE OF PARASITISM IN THE SUBSEQUENT YEAR

BY

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THESIS

Submitted in partial fulfillment of the requirements
for the degree of Master of Science in Natural Resources and Environmental Sciences
in the Graduate College of the
University of Illinois at Urbana-Champaign, 2013

Urbana, Illinois

Advisers:

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ABSTRACT

Brown-headed cowbirds (*Molothrus ater*) rely solely on hosts to raise their young. Although cowbirds parasitize 200+ species, recent evidence suggests that females avoid unsuitable hosts that either reject parasitic eggs or provide incompatible parental care. Female cowbirds may be able to improve their own reproductive success with information pertaining to the fledging success of cowbird or host offspring. This, in turn, could influence the laying decisions and host choices of cowbirds in subsequent years. To determine whether host reproductive success and/or cowbird reproductive success in the previous year affect the likelihood of cowbird parasitism, we examined nesting data for a highly suitable host, the prothonotary warbler (*Protonotaria citrea*). We recorded parasitism status (yes or no), number of cowbird eggs, and the number of host and cowbird fledglings for 3848 warbler nests from 1994-2010 in southern Illinois. Data were analyzed using a generalized linear mixed model (GLMM) with binomial distribution. We accounted for variation in site, nest box, identity of female warbler, and year in our analysis as random effects and included month and the parasitism rate in the previous year as covariates. From one year to the next, the probability of parasitism for a given site increased with cowbird reproductive success and tended to decrease with prothonotary warbler reproductive success even after controlling for the ambient rate of parasitism in the previous breeding season. This is the first study to suggest that the fledging success of cowbirds increases future host use by female cowbirds.

ACKNOWLEDGEMENTS

We thank numerous field assistants who collected data over many years. We also thank Patrick Weatherhead, Jeffrey Brawn, Matthew McKim-Louder, and the University of Illinois Bird Lab for their constructive comments and discussions. Funding for this research was provided by the United States Fish and Wildlife Service, the Illinois Department of Natural Resources, and The Nature Conservancy in Illinois. Finally, we are grateful for logistical support from the Illinois Natural History Survey of the Prairie Research Institute, Cypress Creek National Wildlife Refuge, and the Cache River State Natural Area.

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INTRODUCTION

Obligate avian brood parasites evade nest building, egg incubation, and offspring provisioning by laying eggs in the nests of other species. This behavior is costly for the host species whose reproductive output is diminished (Rothstein 1990; Robinson et al. 1995; Ortega 1998; Lorenzana and Sealy 1999; Hoover 2003c). Interestingly, the reproductive success of brood parasites varies greatly and depends on the host species parasitized (Brooke and Davies 1987; Soler et al. 1995; Scott and Lemon 1996; Rutila et al. 2002; Mermoz and Reboreda 2003; Grim et al. 2011; Trnka et al. 2012). While the parental investment of brood parasites is assumed to cease once the egg is laid, evidence of parasitic females monitoring the fate of their reproductive effort is accumulating (Soler et al. 1995; Arcese et al. 1996; Hoover and Robinson 2007). Females may therefore collect information that influences their future parasitism decisions.

The ability of brood parasites to track their own reproductive output could increase individual fitness if they learn to specialize on high quality hosts. The screaming cowbird (*Molothrus rufoaxillarius*), a host specialist, is thought to preferentially parasitize the bay-winged cowbird (*Agelaioides badius*) because this host provides higher reproductive success than alternative hosts within the community (De Marsico and Reboreda 2008). The brown-headed cowbird (*M. ater*) is an extreme host generalist that parasitizes a suite of hosts within diverse avian communities in many habitats throughout North America (Lowther 1993; Robinson et al. 1993; Davies 2010). These potential hosts differ considerably in their response to cowbird eggs and in their ability to raise cowbird offspring (Mason 1986; Wiley 1988), setting the stage for selection favoring individual female brown-headed cowbirds that use hosts of higher quality in the community.

The quality of potential hosts of brown-headed cowbirds (cowbirds hereafter) largely depends on the likelihood that a particular host species can recognize and reject parasitic eggs, or is in some way incompatible with raising a parasitic egg/chick. Rejecters may thwart raising parasitic young by means of egg ejection, nest desertion, or egg burial (Rothstein 1975). Also, the incubation period, nestling diet, and nestling size of many host species is incompatible with that needed to successfully rear cowbird offspring (Middleton 1977). Evidence of cowbirds avoiding incompatible hosts through non-random host use has been documented in several populations (Alderson et al. 1999; Hahn et al. 1999; Woolfenden et al. 2004; Strausberger and Ashley 2005). During the breeding season and across years, cowbirds preferentially laid eggs in the nests of dickcissels (*Spiza americana*), a species that successfully fledges cowbird young, over other available hosts at Konza Prairie Biological Station (Rivers et al. 2010). Cowbirds have also been shown to select higher quality individuals within a single host population in order to maximize their reproductive output (Grant and Sealy 2002). While cowbirds may be very general in their use of hosts over their geographic distribution, some cowbird populations and/or individual females could focus on relatively few host species depending on which hosts are best at raising parasitic young.

Microsatellite DNA markers have confirmed the presence of host specialization among some individual females within cowbird populations (Alderson et al. 1999; Woolfenden et al. 2003; Strausberger and Ashley 2005). Radio telemetry and genetic studies also indicate high breeding site and home range (primary egg-laying area) fidelity between years (Dufty 1982; Hahn et al. 1999). Cowbird females also monitor host nest contents both before and after parasitism to time the laying of eggs and ensure their acceptance by the host (Hoover and Robinson 2007). Evidence of host preference, in combination with host nest monitoring and site fidelity within cowbird populations, suggests cowbirds could use their own reproductive experience or that of their hosts to improve future breeding decisions.

In this study, we used a long-term nesting dataset from a highly suitable host to investigate factors influencing cowbird parasitism at the population level across years. As a high quality host, the prothonotary warbler (*Protonotaria citrea*; warbler hereafter) accepts cowbird eggs and has an incubation period ideal for cowbird eggs (approximately 12 days) (Petit 1999). Cowbird young are competitive for provisioned food because they are larger than warbler young throughout the nestling and fledgling stage. Warbler young are fed an insectivorous diet by both parents (Hoover and Reetz 2006), which is compatible with the diet required to raise cowbird young. Nest predation is the main factor limiting the warblers' reproductive output (Hoover 2003a) and reduces the success of warbler and cowbird eggs/chicks similarly (Hoover 2003c). Extensive predator proofing of warbler nest boxes on some sites in some years has created considerable variation in rates of nest predation for warblers over time (Hoover 2003a). However, annual and spatial variation in food availability and nest ectoparasites (i.e. blowflies, genus *Protocalliphora*) within warbler nests has sometimes uncoupled the probability of host and cowbird young surviving until fledging (W. Schelsky, personal communication). Cowbird reproductive output has also varied with the intentional removal of parasitic eggs from some warbler nest boxes in some years as the result of concurrent studies within the study system. With this unique dataset, we test whether the reproductive output of warblers and/or cowbirds on a site during a breeding season subsequently influences the probability of cowbird parasitism in the following year.

To determine whether host or parasite reproductive output in one year subsequently influences the rate of cowbird parasitism in the following year we controlled for year, month, site, nest box, and warbler female identity in the season of the parasitism event, and the rate of parasitism on a site in the previous year. Because cowbirds may be responding to current and/or past conditions when selecting hosts to parasitize, warbler density on a site in the current year and the average warbler and cowbird reproductive output from a given site in the previous year were used as predictors of the probability of parasitism. We included warbler density because in some studies host density influenced rates of brood parasitism (Barber and Martin 1997; Woolfenden et al. 2004; Stokke et al. 2007). Because fledging of cowbirds is a better indicator of host quality than fledging of host offspring, we hypothesized that female cowbirds are monitoring and responding to cowbird fledging success rather than the fledging success of the host to improve parasitism decisions in future breeding seasons. Therefore, we predicted that as more cowbird young fledge per warbler nest on a site, the following year's rate of cowbird parasitism for warblers on that site should increase, whereas the number of warbler fledglings per nesting attempt on a site should have relatively little influence on the rate of future cowbird parasitism.

METHODS

Study site and species

The study was conducted over a 17-year period (1994 to 2010) in the Cache River Watershed in southern Illinois, United States. The Cache River meanders 176 km to the Ohio River through 91% of the state's forested wetland and swamp habitat. Study sites were located in agriculturally fragmented patches of forested sloughs and floodplains with bald cypress (*Taxodium distichum*) and tupelo (*Nyssa aquatica*) swamps, within a 192-km^2 portion of the watershed.

Agricultural development and timber harvesting in the Cache during the 1900s provided ideal foraging locations for brown-headed cowbird populations expanding east into the Midwest (Robinson et al. 1999). During the breeding season, female cowbirds travel daily from feeding areas in mowed grasses, pastures, and row-crop agriculture to breeding sites in bottomland forests where they parasitize the nests of a variety of host species. One such host, the prothonotary warbler, is a Neotropical migratory songbird that is territorial and socially monogamous (Petit 1999). These warblers nest in secondary cavities within forested wetlands and swamps and their use of nest boxes provides easy access to nests for monitoring cowbird parasitism status and nesting success. Despite a high rate of cowbird parasitism, the warblers are typically double-brooded and often capable of raising both cowbird and host nestlings in each nesting attempt (Hoover 2003c; Hoover and Robinson 2007). The warblers are a relatively high quality host compared to the other 12 host species that are commonly parasitized by cowbirds within the study area (J. Hoover, personal communication) and can raise up to three cowbird young in one nesting attempt (Hoover 2003b).

Data collection

Each year we set up and monitored approximately 1000 warbler nest boxes across 21 sites (individual patches of suitable breeding habitat for warblers separated by more than 1 km of non-suitable habitat). Nest boxes were made from modified 1.9 L beverage cartons (Fleming and Petit 1986) and placed on trees about 1.7 m above the ground in suitable habitat. Nest boxes were spaced an average of 50 m apart, and openings in boxes were made to be the average diameter (44 mm) of warbler nests in natural cavities allowing cowbird access to each nest. Study sites where the opening size of nest boxes was reduced to exclude parasitism by cowbirds were not included in our analyses. From 1999 to 2010, we removed an estimated 20-100% of cowbird eggs from approximately two thirds of study sites each year. We monitored boxes every 3-5 days from late April to early August 1994-2010. The status of each nesting attempt was recorded, including the number of warbler and cowbird eggs, nestlings, and fledglings as well as the number of cowbird eggs that were removed. We considered nestlings to have fledged if they reached 10-11 days of age and the nest was empty and intact on the subsequent visit. Additional evidence of fledging included the presence of trampled droppings in the nest, alarm calls from adults, and observations of appropriately-aged fledglings in the territory. The fate of each nesting attempt was known and recorded throughout each breeding season.

Statistical analyses

The probability of cowbird parasitism, a binary response variable, was analyzed using a generalized linear mixed model (GLMM) with Laplace approximation of the log likelihood (Bolker et al. 2009) and an identity link function (GLIMMIX; SAS 9.2). To account for variation associated with year, site, nest box identity, and female warbler identity, we included each as a random variable. For female warbler identity, we included a subset of nests where the female warbler identity was unknown (21% of all nesting attempts). These nests were always those that failed or were abandoned early in the nesting cycle and eliminating these from our dataset would have significantly reduced the variation in both the cowbird and host reproductive success variables. We also included month (April-July) as a categorical variable to account for the seasonal decline in cowbird parasitism known to occur in our study system (Hoover et al. 2006). In order to control for landscape-level effects of cowbird parasitism in our analyses, such that high parasitism in one year leads to high or higher parasitism in the next because of the configuration of forest habitat and cowbird foraging areas (Goguen and Matthews 2000; Hoover and Hauber 2007), we included the ambient parasitism rate from each site from the previous year (number of warbler nests parasitized/number of warbler nesting attempts per site). We included warbler density (number of females/hectare/site) to investigate if a current condition such as the density of a quality host predicts the probability of cowbird parasitism in the same year. Cowbird egg removal in the previous year (cowbird eggs removed/cowbird eggs laid/site) was included in our analyses because the removal of a portion of the parasitic eggs on certain sites in some years may influence future parasitism rates by altering the reproductive output of both cowbirds and warblers. Finally, to test whether host or cowbird reproductive success best predicted cowbird parasitism in the subsequent year, we included warbler reproductive success for the previous year (number of warblers fledged/number of warbler nesting attempts/site), and cowbird reproductive success for the previous year (number of cowbirds fledged/number of warbler nesting attempts/site).

We used Akaike's information criterion, corrected for small sample size (AIC_C), to identify the model that best explained cowbird parasitism rates for the prothonotary warbler (Burnham and Anderson 2002). We assembled a set of *a priori* candidate models based on our hypotheses and analyzed them using SAS 9.2 (SAS Institute, Inc., Cary, NC, USA). Each model included month to control for the seasonal decline in parasitism and ambient rate of parasitism in the previous year to control for landscape-level effects on parasitism. We did not include correlated explanatory variables ($r > 0.50$) in the same model to reduce any effects of collinearity among variables. The only variables to violate this assumption were cowbird egg removal and cowbird reproductive success both from the previous year ($r = 0.51$). In this case we moved forward with cowbird reproductive success from the previous year in our *a priori* models because this variable encapsulated the variation associated with cowbird egg removal and all other ecological factors that contribute to cowbird reproductive success. In addition, we removed cowbird eggs only during a subset of all of the years included in our analyses. The models were ranked in order of their AIC_C values, with the highest explanatory value given to models with the lowest AIC_C values and highest Akaike weight (w_i). To determine whether cowbird egg removal or cowbird reproductive success from the previous year better explained parasitism rates we compared the top ranked model that contained cowbird reproductive success to the same model replacing cowbird success with cowbird egg removal. Parameter estimates, standard errors, and 95% CI are based on model averages. All descriptive variables are presented as means ± SD unless otherwise indicated.

We also investigated whether there was any indication that female cowbirds focused their current parasitism on particular female warblers or nest boxes for those nest boxes that successfully fledged a cowbird in the previous year. To determine this we used a reduced dataset to compare parasitism status (yes, no) among three categories of nests for first nesting attempts within a given year. These categories of nests were: 1) same female warbler in same nest box as the previous year, 2) same female using a different nest box than the previous year but still in the study site, and 3) new female in a nest box that had fledged a cowbird in the previous year. If female cowbirds focused on particular female warblers that had successfully raised a cowbird in the previous year, then categories 1 and 2 should have higher rates of parasitism than category 3. If instead female cowbirds focused on particular nest boxes that had fledged a cowbird in the previous year, then categories 2 and 3 should have higher rates of parasitism than category 1. We used a chi-square test to compare the frequency of parasitism among the three categories of nests.

RESULTS

Of the 3848 warbler nests included in our analyses, 2240 (58%) were parasitized by brown-headed cowbirds. Parasitized warbler nests received an average of 1.73 ± 0.52 cowbird eggs, with 0.24 ± 0.25 cowbird young fledging from parasitized nests. Overall, 39% of warbler nesting attempts successfully fledged cowbird and/or host young between 1994 and 2010. Female cowbirds laid 3885 eggs in warbler nests, of which 18% survived to fledge.

The top ranked model predicting the probability of parasitism for prothonotary warblers included month (M), parasitism rate in the previous year (PPR), warbler reproductive success in the previous year (PWS), and cowbird reproductive success in the previous year (PCS)(Model 1; Table 1). The sum of weights (*w*i) for all models that included cowbird reproductive success in the previous year was 0.80 indicating that this variable was one of the most important ones tested (Table 2). Month was included in all the models and the probability of parasitism decreased seasonally from 92% in April to 11% in July (Figure 1). The rate of parasitism in the previous year was also included in all the models and as expected was positively correlated with parasitism in the current year (Figure 2). Cowbird parasitism of warblers increased with an increase in cowbird fledging success in the previous year, and ranged from 51% when there was little or no cowbird fledging success the previous year to 70% when cowbird fledging success the previous year was high (nearly one cowbird fledged per nesting attempt; Figure 3).

Warbler reproductive output (PWS) was included in two of the top three models and therefore, may be an important predictor of parasitism rate (*w*i = 0.68). In contrast to cowbird reproductive success, warbler reproductive success was negatively related to the probability of parasitism and the model averaged 95% CI of the β estimate overlapped zero. This suggests that PWS may have little overall influence on parasitism rates. Although warbler density (*w*i = 0.30) was included in the second top model (Model 2; Table 1), the ΔAICc = 1.67 and model averaged 95% CI of the β estimates bounded zero, indicating that warbler density added little to explain variation in the data given the other variables tested. Because cowbird egg removal was correlated with cowbird reproductive success (r = 0.51), we substituted cowbird egg removal into the top-ranked model. This model was not well supported and the removal of cowbird eggs did a poorer job than cowbird reproductive success to explain variation in the probability of parasitism as it was ranked lower than the top model (ΔAICc = 0.22) and the 95% CI of the β estimates bounded zero (UCL = 0.140, LCL = -0.818). The analysis of female warblers and nest boxes that fledged a cowbird in the previous year and their parasitism status in the subsequent year indicated no significant difference in parasitism status among the three categories of nesting attempts (X^2 = 0.715, n= 915, d.f. = 2, p = 0.699; Category 1 = 61%, Category 2 = 57%, Category 3 rate = 59%).

DISCUSSION

The probability of parasitism for prothonotary warblers increased with cowbird reproductive success in the previous year, even after controlling for other factors (previous parasitism rate and month) known to be important in our study system. This result suggests that host use by cowbird females is not merely a function of forest fragmentation and landscape use by cowbirds, but rather that female cowbirds may attempt to maximize reproductive success through active host choice. However, it is unclear if the observed correlation between cowbird reproductive success in one year and parasitism rate in the next is the result of adult cowbird females using breeding information from one year to make future breeding decisions or, alternatively, the local recruitment of cowbird offspring.

Female cowbirds may draw upon their own breeding experience or that of other cowbird females to make future host-use decisions because the fitness of brood parasites depends on the ability of the host to rear parasitic young. By using their own reproductive success (i.e. private information), the success of conspecifics (i.e. public information), or both, females could potentially increase their reproductive output across years by targeting productive sites and hosts. The use of private and public information in future breeding decisions has been widely investigated in non-parasitic passerines (Doligez et al. 2002; Hoover 2003a; Danchin et al. 2004), but data are limited for brood parasitic species. The use of private information could lead to greater host specificity within individual females as they hone their ability to choose host species that are better able to fledge parasitic young during several consecutive breeding seasons. Furthermore, females could collect public information regarding the breeding habitat, nest type, or other natural history characteristics of hosts that successfully rear cowbird offspring (Mahler et al. 2007). This may lead to the immigration of adult female cowbirds into habitat patches where warblers are breeding, thereby increasing the number of cowbirds and, consequently, the probability of parasitism for warblers.

Parasitism of warblers may increase with cowbird fledging success in the previous year because juvenile cowbirds may be site or host faithful and return to their natal location and/or host species to breed in subsequent years. Therefore, local recruitment of cowbird offspring alone could account for the rise in parasitism with increasing cowbird reproductive success. Juveniles may preferentially parasitize the species that raised them by imprinting on the host species itself (Brooke and Davies 1987; Payne and Payne 1998; Payne et al. 2000), on the nest characteristics of that species (Kattan 1997; Mahler et al. 2007), or on the habitat it was raised in (Teuschl et al. 1998). A cavity nesting passerine, the prothonotary warbler could offer cowbirds a unique nestling experience and search image compared to other available species in the host community. However, while adult brood parasites display both seasonal (Soler et al. 1995; Hoover and Robinson 2007; Langmore et al. 2007) and between-year (Dufty 1982; Raim 2000) breeding site fidelity, natal philopatry for cowbirds is considered rare (Alderson et al. 1999; Hauber et al. 2012). Therefore, the observed increase in the probability of parasitism with cowbird reproductive success is not likely explained by the local recruitment of cowbird offspring alone. In fact, only 1 (<<1%) of the approximately 610 cowbird nestlings that were banded and fledged from prothonotary warbler nest boxes in our study system has been captured in a later breeding season (M. McKim-Louder, personal communication), suggesting that local recruitment for cowbird juveniles in our system is rare and not the cause of our observed increase in the rate of cowbird parasitism.

One might expect cowbirds generally to parasitize hosts that experience low rates of nest predation and high fledging success of host young, particularly if cowbirds are able to assess that the presence of many host fledglings on a site is a function of low rates of nest predation. Low rates of nest predation associated with these hosts could lead to reduced cowbird nestling mortality and aid in bolstering existing cowbird populations. Conversely, our results indicate that warbler reproductive output is not a good predictor of cowbird parasitism in the subsequent breeding season. This suggests that, in our system, the fledging of host young is not the best information used in host selection by female cowbirds; however, it may be useful for cowbirds in some habitats with exceedingly high rates of nest predation for most host species (Winfree et al. 2006).

Warbler density in the current year was examined as a potential predictor of cowbird parasitism to investigate if female cowbirds parasitize warblers based on their availability (Woolfenden et al. 2004), instead of their ability to fledge cowbird young. While warbler density was not a good predictor of parasitism and had little influence in our study system, evidence exists for common cuckoos (*Cuculus canorus)* (Stokke et al. 2007) and Horsfield's bronze cuckoos (*Chrysococcyx basalis)* (Brooker and Brooker 2003), both host specialists. In both cases, cuckoos avoid specific host populations with host densities below a certain threshold. Alternatively, for generalist parasites, landscape features can override the effects of host density. In plumbeous vireos (*Vireo plumbeus*), for example, brown-headed cowbird parasitism was related to proximity to parasite feeding areas but not to host density (Goguen and Mathews 2000). Woolfenden et al. (2004) reported that host density was a predictor of parasitism by cowbirds for yellow warblers (*Dendroica petechia*) and red-winged blackbirds (*Agelaius phoenecius*), but was not a factor for the most frequently parasitized and highest value host, the song sparrow (*Melospiza melodia*). The influence of host density on patterns of parasitism may vary depending on the host specificity of the brood parasite and/or the quality of the host species parasitized. The rate of cowbird parasitism for prothonotary warblers could fluctuate in response to changes in the availability of alternative hosts, but we did not measure changes in the densities or rates of cowbird parasitism of other hosts during the course of this study. Nevertheless, it is difficult to imagine how the availability of alternative hosts in the current year could fluctuate in parallel with cowbird reproductive success in a way that would undermine the effect of PCS on cowbird parasitism of the warblers.

Our results suggest that the rate of parasitism for a high quality host was best predicted by brown-headed cowbird reproductive success in the previous year. This implies cowbird females are likely monitoring cowbird reproductive output to make future breeding decisions. One or a combination of factors may result in the increased rate of parasitism for warblers observed during this study, and it remains to be determined whether this pattern is being driven more by greater host specificity among local cowbird females returning to the same breeding areas across years, the immigration of adult female cowbirds into warbler breeding areas, or local recruitment of cowbird offspring produced by the warblers. Female cowbirds do not preferentially parasitize particular female warblers or nest boxes that fledged a cowbird in the previous year. This result suggests that cowbird females in our study system are not necessarily tracking individual female warblers or nest boxes across years, but may be tracking cowbird production by this host species at the scale of female cowbird egg-laying ranges within a study site (which encompass several warbler territories) or the entire study site. Female cowbirds likely are using some combination of private and public information, associated with their and other female cowbird's success with this particular host, to modify their egg-laying decisions and host specificity from one breeding season to the next.

Evidence of a generalist brood parasite using breeding information across years to enhance reproductive output provides new insights into the evolution of host specificity in obligate brood parasites. Efforts to manage parasite populations for threatened or endangered host species could possibly reduce the fledging success of parasitic young to curb parasitism attempts in subsequent years; however, this should be used with caution because new individuals can immigrate into and continually replace the experienced cowbird population. Future experimental research involving genetic analyses should help to determine the roles of private and public information in female cowbird host-use decisions and whether increases in parasitism are associated with repeated parasitism from known individuals versus an influx of new or young cowbird females.

REFERENCES

Alderson GW, Gibbs HL, Sealy SG (1999) Determining the reproductive behaviour of individual brown-headed cowbirds using microsatellite DNA markers. Animal Behaviour 58:895-905

Arcese P, Smith JNM, Hatch MI (1996) Nest predation by cowbirds and its consequences for passerine demography. Proceedings of the National Academy of Sciences of the United States of America 93:4608-4611

Barber DR, Martin TE (1997) Influence of alternative host densities on brown-headed cowbird parasitism rates in black-capped vireos. The Condor 99:595-604

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White JSS (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends in Ecology & Evolution 24:127-135

Brooke MD, Davies NB (1987) Recent changes in host usage by cuckoos *Cuculus canorus* in Britain. Journal of Animal Ecology 56:873-883

Brooker M, Brooker L (2003) Brood parasitism by horsfield's bronze-cuckoo in a fragmented agricultural landscape in Western Australia. Emu 103:357-361

Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. Springer-Verlag, New York

Danchin É, Giraldeau L-A, Valone TJ, Wagner RH (2004) Public information: from nosy neighbors to cultural evolution. Science 305:487-491

De Marsico MC, Reboreda JC (2008) Differential reproductive success favours strong host preference in a highly specialized brood parasite. Proceedings of the Royal Society B-Biological Sciences 275:2499-2506

Doligez B, Danchin E, Clobert J (2002) Public information and breeding habitat selection in a wild bird population. Science 297:1168-1170

Dufty AM (1982) Movements and activities of radio-tracked brown-headed cowbirds. Auk 99:316-327

Fleming WJ, Petit DR (1986) Modified milk carton nest box for studies of prothonotary warblers. Journal of Field Ornithology 57:313-315

Goguen CB, Mathews NE (2000) Local gradients of cowbird abundance and parasitism relative to livestock grazing in a western landscape. Conservation Biology 14:1862-1869

Grant ND, Sealy SG (2002) Selection of red-winged blackbird (*Agelaius phoeniceus*) hosts by the brown-headed cowbird (*Molothrus ater*). Bird Behavior 15:21-30

Grim T, Samas P, Moskat C, Kleven O, Honza M, Moksnes A, Roskaft E, Stokke BG (2011) Constraints on host choice: why do parasitic birds rarely exploit some common potential hosts? Journal of Animal Ecology 80:508-518

Hahn DC, Sedgwick JA, Painter IS, Casna NJ (1999) A spatial and genetic analysis of cowbird host selection. In: Morrison ML, Hall LS, Robinson SK, Rothstein SI, Hahn DC, Rich TD (eds) Research and Management of the Brown-headed Cowbird in Western Landscapes, pp 204-217

Hauber ME, Strausberger BM, Feldheim KA, Lock J, Cassey P (2012) Indirect estimates of breeding and natal philopatry in an obligate avian brood parasite. Journal of Ornithology 153:467-475

Hoover JP (2003a) Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology 84:416-430

Hoover JP (2003b) Experiments and observations of prothonotary warblers indicate a lack of adaptive responses to brood parasitism. Animal Behaviour 65:935-944

Hoover JP (2003c) Multiple effects of brood parasitism reduce the reproductive success of prothonotary warblers, *Protonotaria citrea*. Animal Behaviour 65:923-934

Hoover JP, Reetz MJ (2006) Brood parasitism increases provisioning rate, and reduces offspring recruitment and adult return rates, in a cowbird host. Oecologia 149:165-173

Hoover JP, Yasukawa K, Hauber ME (2006) Spatially and temporally structured avian brood parasitism affects the fitness benefits of hosts' rejection strategies. Animal Behaviour 72:881-890

Hoover JP, Hauber ME (2007) Individual patterns of habitat and nest-site use by hosts promote transgenerational transmission of avian brood parasitism status. Journal of Animal Ecology 76:1208-1214

Hoover JP, Robinson SK (2007) Retaliatory mafia behavior by a parasitic cowbird favors host acceptance of parasitic eggs. Proceedings of the National Academy of Sciences 104:4479-4483

Kattan GH (1997) Shiny cowbirds follow the 'shotgun' strategy of brood parasitism. Animal Behaviour 53:647-654

Langmore NE, Adcock GJ, Kilner RM (2007) The spatial organization and mating system of horsfield's bronze-cuckoos, *Chalcites basalis*. Animal Behaviour 74:403-412

Lorenzana JC, Sealy SG (1999) A meta-analysis of the impact of parasitism by the brown-headed cowbird on its hosts. Studies in Avian Biology 18:241-253

Lowther PE (1993) Brown-headed cowbird (*Molothrus ater*). In: Poole A, Gill, F. (ed) The Birds of North America. Cornell Lab of Ornithology, Ithaca

Mahler B, Confalonieri VA, Lovette IJ, Reboreda JC (2007) Partial host fidelity in nest selection by the shiny cowbird (*Molothrus bonariensis*), a highly generalist avian brood parasite. Journal of Evolutionary Biology 20:1918-1923

Mason P (1986) Brood parasitism in a host generalist, the shiny cowbird: I. The quality of different species as hosts. Auk 103:52-60

Mermoz ME, Reboreda JC (2003) Reproductive success of shiny cowbird (*Molothrus bonariensis*) parasitizing the larger brown-and-yellow marshbird (*Pseudoleistes virescens*) in Argentina. Auk 120:1128-1139

Middleton ALA (1977) Effect of cowbird parasitism on American goldfinch nesting. Auk 94:304-307

Ortega CP (1998) Cowbirds and other brood parasites. University of Arizona Press

Payne RB, Payne LL (1998) Brood parasitism by cowbirds: risks and effects on reproductive success and survival in indigo buntings. Behavioral Ecology 9:64-73

Payne RB, Payne LL, Woods JL, Sorenson MD (2000) Imprinting and the origin of parasite-host species associations in brood-parasitic indigobirds, *Vidua chalybeata*. Animal Behaviour 59:69-81

Petit LJ (1999) Prothonotary warbler, *Prothonotaria citrea*. In: Poole A, Gill, F. (ed) The Birds of North America, Philadelphia

Raim A (2000) Spatial patterns of breeding female brown-headed cowbirds on an Illinois site. University of Texas Press

Rivers JW, Jensen WE, Kosciuch KL, Rothstein SI (2010) Community-level patterns of host use by the brown-headed cowbird (*Molothrus ater*), a generalist brood parasite. Auk 127:263-273

Robinson SK, Brawn JD, Morse SF, Herkert JR (1999) Use of different habitats by breeding brown-headed cowbirds in fragmented midwestern landscapes. Studies in Avian Biology 18:52-61

Robinson SK, Grzybowski JA, Rothstein SI, Brittingham MC, Petit LJ, Thompson FR (1993) Management implications of cowbird parasitism on Neotropical migrant songbirds. U S Forest Service General Technical Report RM 229:93-102

Robinson SK, Thompson FR, Donovan TM, Whitehead DR, Faaborg J (1995) Regional forest fragmentation and the nesting success of migratory birds. Science 267:1987-1990

Rothstein SI (1975) Evolutionary rates and host defenses against avian brood parasitism. American Naturalist 109:161-176

Rothstein SI (1990) A model system for coevolution: avian brood parasitism. Annual Review of Ecology and Systematics 21:481-508

Rutila J, Latja R, Koskela K (2002) The common cuckoo *Cuculus canorus* and its cavity nesting host, the redstart *Phoenicurus phoenicurus*: a peculiar cuckoo-host system? Journal of Avian Biology 33:414-419

Scott DM, Lemon RE (1996) Differential reproductive success of brown-headed Ccowbirds with northern cardinals and three other hosts. Condor 98:259-271

Soler JJ, Soler M, Moller AP, Martinez JG (1995) Does the great spotted cuckoo choose magpie hosts according to their parenting ability? Behavioral Ecology and Sociobiology 36:201-206

Stokke BG, Hafstad I, Rudolfsen G, Bargain B, Beier J, Campas DB, Dyrcz A, Honza M, Leisler B, Pap PL, Patapavicius R, Prochazka P, Schulze-Hagen K, Thomas R, Moksnes A, Moller AP, Roskaft E, Soler M (2007) Host density predicts presence of cuckoo parasitism in reed warblers. Oikos 116:913-922

Strausberger BM, Ashley MV (2005) Host use strategies of individual female brown-headed cowbirds *Molothrus ater* in a diverse avian community. Journal of Avian Biology 36:313-321

Trnka A, Pozgayova M, Prochazka P, Prokop P, Honza M (2012) Breeding success of a brood parasite is associated with social mating status of its host. Behavioral Ecology and Sociobiology 66:1187-1194

Weatherhead PJ, Forbes MRL (1994) Natal philopatry in passerine birds: genetic or ecological influences? Behavioral Ecology 5:426-433

Wiley JW (1988) Host selection by the shiny cowbird. Condor 90:289-303

Winfree R, Dushoff J, Robinson SK, Bengali D (2006) A Monte Carlo model for estimating the productivity of a generalist brood parasite across multiple host species. Evolutionary Ecology Research 8:213-236

Winkler DW, Wrege PH, Allen PE, Kast TL, Senesac P, Wasson MF, Sullivan PJ (2005) The natal dispersal of tree swallows in a continuous mainland environment. Journal of Animal Ecology 74:1080-1090

Woolfenden BE, Gibbs HL, McLaren CM, Sealy SG (2004) Community-level patterns of parasitism: Use of three common hosts by a brood parasitic bird, the brown-headed cowbird. Ecoscience 11:238-248

Woolfenden BE, Gibbs HL, Sealy SG, McMaster DG (2003) Host use and fecundity of individual female brown-headed cowbirds. Animal Behaviour 66:95-106

TABLES AND FIGURES

Table 1. Model selection to estimate probability of parasitism of prothonotary warblers, *Protonotaria citrea*, by brown-headed cowbirds, *Molothrus ater*, in southern Illinois, USA, 1994-2010.

No.	Model	AIC_C	ΔAIC_C	w_i	K	-2LL
1	M+PPR+PWS+PCS	4196.84	0.00	0.40	9	3780.77
2	M+PPR+PWS+PCS+Wdensity	4198.51	1.67	0.18	10	3778.28
3	M+PPR+PCS	4198.72	1.88	0.16	8	3770.41
4	M+PPR	4200.26	3.42	0.07	7	3779.78
5	M+PPR+PWS	4200.39	3.55	0.07	8	3770.29
6	M+PPR+PCS+Wdensity	4200.73	3.89	0.06	9	3773.06
7	M+PPR+PWS+Wdensity	4201.74	4.90	0.03	9	3776.34
8	M+PPR+Wdensity	4202.15	5.31	0.03	8	3771.04

M, month incubation of nesting attempt initiated (April-July); PPR, ambient rate of parasitism per site in previous year; PWS, number of warblers fledge per warbler nesting attempt per site in the previous year; PCS, number of cowbirds fledged per warbler nesting attempt per site in the previous year; Wdensity, density of warblers in a given site in the current year; AIC_C, Akaike's information criterion corrected for small sample size; $\Delta_i = AIC_{C(i)} - AIC_{C(min)}$; w_i, Akaike weight; K, number of explanatory parameters in the model; -2LL, -2 log-likelihood.

Table 2. Average parameter estimates with standard errors and parameter likelihood are shown for all models.

No.	Int	M	PPR	PWS	PCS	Wdensity
1	8.003 (0.521)	-1.525 (0.078)	1.233 (0.380)	-0.174 (0.087)	1.319 (0.553)	
2	7.944 (0.531)	-1.527 (0.078)	1.202 (0.384)	-0.188 (0.091)	1.287 (0.556)	0.051 (0.088)
3	7.667 (0.493)	-1.530 (0.078)	1.577 (0.341)		1.020 (0.540)	
4	7.787 (0.496)	-1.531 (0.078)	1.694 (0.338)			
5	8.036 (0.530)	-1.528 (0.078)	1.486 (0.369)	-0.116 (0.084)		
6	7.666 (0.513)	-1.530 (0.078)	1.577 (0.341)		1.019 (0.548)	0.001 (0.084)
7	7.925 (0.539)	-1.530 (0.078)	1.434 (0.375)	-0.139 (0.089)		0.072 (0.089)
8	7.735 (0.519)	-1.532 (0.078)	1.690 (0.338)			0.029 (0.084)
Model Averaged Parameter Estimates						
β	7.83	-1.53	1.37	-0.17	1.23	-0.04
β LCL	6.86	-1.68	0.57	-0.35	0.12	-0.13
β UCL	8.79	-1.37	2.17	0.01	2.34	0.23
Sum of w_i				0.68	0.80	0.30

Int, intercept; M, month; PPR, ambient rate of parasitism per site in previous year; PWS, number of warblers fledged per warbler nesting attempt per site in the previous year; PCS, number of cowbirds fledged per warbler nesting attempt per site in the previous year; Wdensity, density of warblers in a given site in the current year; Sum of w_i, sum of Akaike weight.

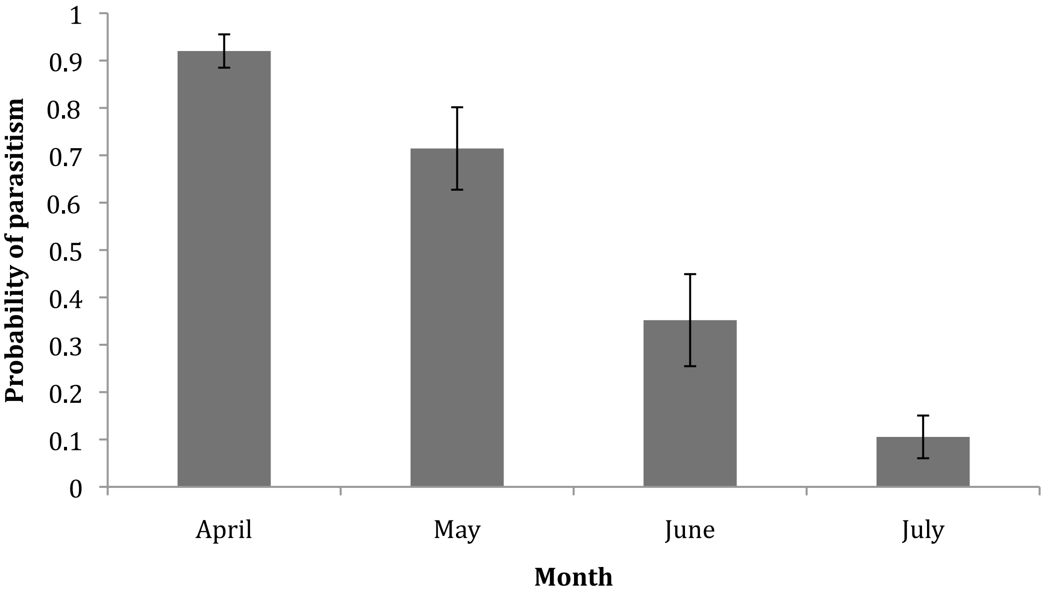

Figure 1. Model averaged mean with 95% CI probability of parasitism by brown-headed cowbirds for prothonotary warblers by month, 1994-2010.

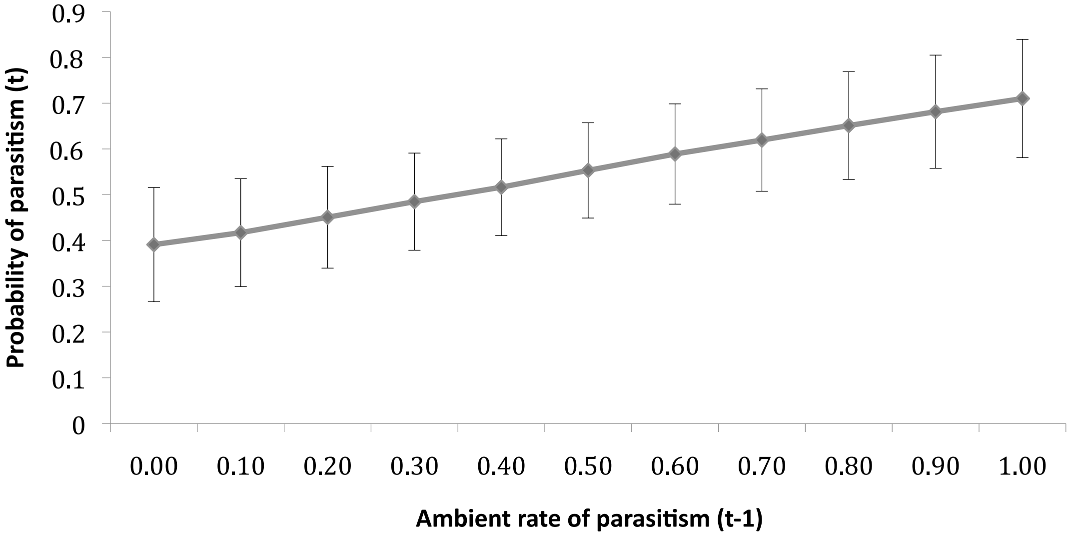

Figure 2. Model averaged mean with 95% CI probability of parasitism by brown-headed cowbirds in year (t) for prothonotary warblers based on ambient parasitism in previous year (t-1), 1994-2010.

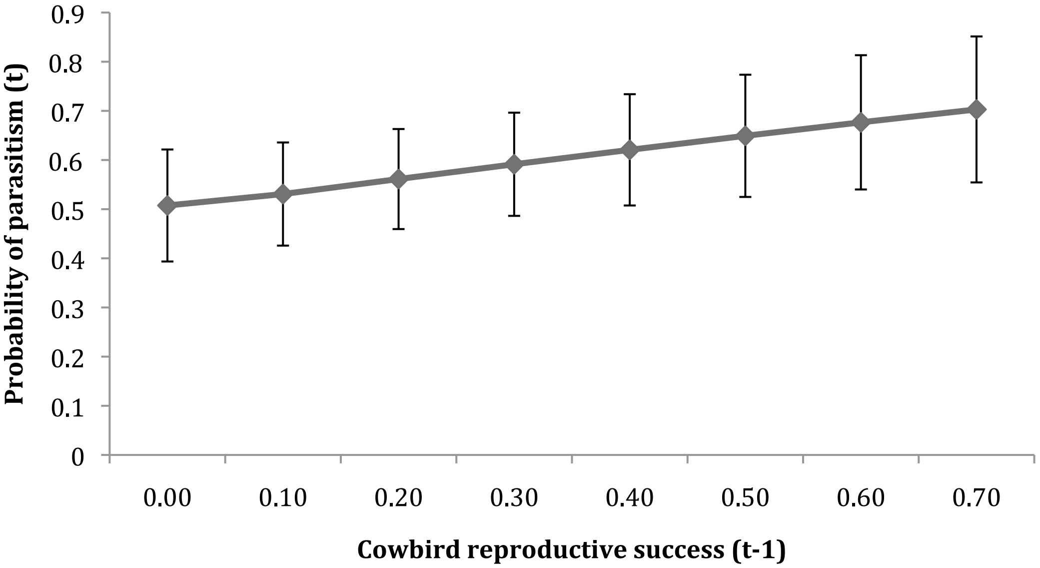

Figure 3. Model averaged mean with 95% CI probability of parasitism by brown-headed cowbirds in year (t) for prothonotary warblers based on cowbird reproductive success in previous year (t-1), 1994-2010.

Juvenile Survival in a Neotropical Migratory Songbird Is Lower than Expected

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Abstract

Attempts to estimate and identify factors influencing first-year survival in passerines, survival between fledging and the first reproductive attempt (i.e. juvenile survival), have largely been confounded by natal dispersal, particularly in long-distance migratory passerines. We studied Prothonotary Warblers (*Protonotaria citrea*) breeding in nest boxes to estimate first-year survival while accounting for biases related to dispersal that are common in mark-recapture studies. The natal dispersal distribution (median = 1420 m; *n* = 429) and a distance-dependent recruitment rate, which controls for effects of study site configuration, both indicated a pattern of short-distance natal dispersal. This pattern was consistent with results of a systematic survey for birds returning outside the nest box study sites (up to 30 km in all directions) within a majority (81%) of total available bottomland forest habitat, further suggesting that permanent emigration outside of the study system was rare. We used multistate mark-recapture modeling to estimate first-year survival and incorporated factors thought to influence survival while accounting for the potential confounding effects of dispersal on recapture probabilities for warblers that fledged during 2004–2009 (*n* = 6093). Overall, the average first-year survival for warblers reared without cowbird nestmates was 0.11 (95% CI = 0.09–0.13), decreased with fledging date (0.22 early to 0.03 late) and averaged 40% lower for warblers reared with a brood parasite nestmate. First-year survival was less than half of the rate thought to represent population replacement in migratory passerines (~0.30). This very low rate suggests that surviving the first year of life for many Neotropical migratory species is even more difficult than previously thought, forcing us to rethink estimates used in population models.

Citation: McKim-Louder MI, Hoover JP, Benson TJ, Schelsky WM (2013) Juvenile Survival in a Neotropical Migratory Songbird Is Lower than Expected. PLoS ONE 8(2): e56059. doi:10.1371/journal.pone.0056059

Editor: Katherine Renton, Universidad Nacional Autonoma de Mexico, Mexico

Received October 11, 2012; **Accepted** January 4, 2013; **Published** February 8, 2013

Funding: Financial support was provided by the United States Fish and Wildlife Service (INT 1448-0003-95-1007), The Nature Conservancy, the Illinois Department of Natural Resources Wildlife Preservation Fund, the University of Illinois, the North American Bluebird Society, the Champaign County and Decatur Audubon Societies, and Sigma Xi. The funders had no role in study design, data collection and analysis, decision to publish, or preparation of the manuscript.

Competing Interests: The authors have declared that no competing interests exist.

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Introduction

Quantifying age-specific survival is necessary to identify factors affecting population growth and to model population dynamics. As juvenile survival is often thought to be lower and more variable than adult survival, estimating the mortality rate of juveniles can provide insights into reproductive tradeoffs and the evolution of life histories [1–3]. For birds, survival between fledging and reproduction (i.e. first-year survival in passerines) is an important life stage considered influential to population growth [4–6], yet it remains a "black box" of avian demography [2] because of the challenges associated with studying survival.

High mortality rates soon after fledging [7,8] and natal dispersal typically confound efforts to accurately quantify first-year survival [9]. For many bird species, small body size prevents using radio-telemetry technology to estimate annual survival. Instead, mark-recapture methods are used to estimate survival of small avian species while accounting for imperfect detection [10]. However, one limitation of mark-recapture methods for estimating first-year survival is that there is no way to differentiate between permanent emigration and mortality [9]. As natal dispersal may lead to considerable rates of permanent emigration, particularly from study systems limited in size, first-year survival estimates are thought to be biased low.

The effects of natal dispersal on survival estimates may be particularly evident in migratory passerines, which annually fly vast distances between breeding and non-breeding locations. For example, typically <7% of migratory passerine nestlings banded in one year are resighted or recaptured within study populations in subsequent breeding seasons [11]. Based on the assumption that adult survival is approximately 0.60 for migratory passerines (reviewed in [12]), population modelers have generally used theoretical rates thought to represent population replacement, such as one-half of adult survival or ~0.30 [13,14]. Why then do studies commonly find local recruitment lower than the expected 0.30 value?

The natal dispersal distances (i.e. straight-line distance between fledging and first breeding locations) of migratory songbirds are thought to be greater than that of their non-migratory counterparts [15,16], which may result in the increased probability of permanent emigration and reduced recruitment into their populations of origin. However, determining natal dispersal distances in migratory passerines has been difficult because of limitations in sample and study system sizes, and a general pattern of decreasing resight or recapture probabilities of dispersers with increasing distance, particularly when study areas are surrounded by vast available habitat [17]. Therefore, it remains unclear whether low juvenile return rates are caused by low survival or permanent emigration.

Incorporating the effects of dispersal into study design and statistical methodology is necessary to increase the accuracy of juvenile survival estimates [9,18]. Likewise, accounting for dispersal is necessary to effectively investigate factors influencing first-year survival. One approach for dealing with the potential influence of dispersal on recapture probability is multistate modeling. This extension of the Cormack-Jolly-Seber model estimates the state-specific (e.g. location, reproductive status, behavior) probability of survival, recapture, and the likelihood of switching between states (transition probability) [19]. Because the detectability of an individual may vary as a function of numerous factors (e.g. time, age, gender, location), multistate modeling is a useful tool to account for potential biases generated by state-dependent recapture probabilities and uncertainty in state identity for occasions when the individual is not observed.

We estimated first-year survival of a Neotropical migratory passerine, the Prothonotary Warbler (*Protonotaria citrea*). First, using a long-term (1995–2010) breeding population we determined the distribution of natal dispersal distances. A distance-dependent recruitment rate was compiled to reduce confounds of nest box configuration on dispersal distances [20]. Further, to determine whether natal dispersal distances calculated from our study were a result of limitations associated with the size of the study system, we expanded the search for banded recruits by systematically searching outside the nest box study area (30 km in all directions) during 2008 and 2009. The habitat specificity of this species allowed us to systematically survey for dispersers within a majority of suitable breeding habitat. Then, by defining natal dispersal distances as states in a multistate framework, we studied several factors that may affect first-year survival while simultaneously controlling for the potential effects of natal dispersal distance on recapture probabilities. We examined whether recapture probabilities were influenced by natal dispersal distances, predicting that recapture probabilities would decrease with dispersal distance. Next, while accounting for potential effects of natal dispersal distances on resight or recapture probabilities, we included variables thought to influence survival rates: effects of season (fledging date), brood parasitism status (reared with or without a cowbird nestmate), nestling body condition, and brood size, to determine an overall first-year survival rate estimate for individuals in our study population.

Methods

Study area and species

The 4,875 km^2 study area was located in southern Illinois and western Kentucky, U.S.A., and was divided into three regions: nest box sites, core, and outside-core areas (Figure 1) (see descriptions below). Prothonotary Warblers are long-distance migrants that winter in the Neotropics and breed in the eastern portion of the United States. These warblers are cavity nesters that breed almost exclusively near or over water within forested wetlands [21], and breed from late April to early August in our study area. Prothonotary Warblers readily use nest boxes when available and are commonly parasitized by an obligate brood parasite, the Brown-headed Cowbird (*Molothrus ater*) [22,23].

Data collection

During 1995–2010, we monitored approximately 1500 nest boxes distributed among 20–25 sites within an approximately 18 by 12 km area. Typically less than half of the nest boxes were used in a given year, suggesting that nest sites were not limiting. Within each site, we placed nest boxes 40–50 m apart within appropriate habitat. Nest boxes were attached to trees, placed 1.7 m above ground and had 44-mm-diameter openings, similar to the attributes of natural cavities used by warblers in this study system [24]. From 1999–2010, a majority of the nest boxes were removed from trees and attached to greased conduit poles to reduce nest predation. We monitored nest boxes every 3–6 days throughout the breeding season and recorded the number of warbler and cowbird eggs and nestlings present each visit. Prior to fledging (age 5–8 days), we banded each nestling's right leg with a uniquely numbered aluminum U.S. Geological Survey band, and measured mass (±0.25 g) and tarsus length (±0.5 mm). We assumed nestlings fledged if they reached 10–11 days of age and the nest was empty and intact. Additional evidence of fledging included the presence of trampled droppings in the nest, alarm calls from adults, and observations of appropriately aged fledglings in the territory. Nestlings that did not survive to fledge were not used in analyses.

We identified banded recruits, individuals banded as nestlings that returned to breed in a subsequent year, as those individuals having a single aluminum band on the right leg. Once captured, we determined the origin of each banded recruit and determined their dispersal distance by measuring the straight-line distance between natal nest box and first recapture location. Nest boxes and recapture locations were recorded with a global positioning system (GPS) unit or identified on topographic maps, accurate to approximately 25 m. Male recruits were captured using audio playback with a decoy placed next to a mist-net and female recruits were captured by placing a small plastic bag over the nest box opening while they were incubating. We marked all banded recruits and other breeding adults with unique combinations of colored leg bands. We assigned adults to active nests based on territorial behavior and their presence at individual nest boxes; each year we knew the identity of >95% of the adults on each nest box study site.

Systematic survey for banded recruits off nest box study sites. In addition to the information collected from the nest box study sites, we conducted a systematic survey between 15 May and 4 July in 2008 and 2009 to locate banded recruits of all ages outside of the nest box study sites. We defined the core survey area as all suitable breeding habitat located in the areas between nest box sites and within a 5-km buffer surrounding the nest box sites (Figure 1). Suitable breeding habitat located from 5 km to 30 km surrounding the core survey area was defined as outside-core (Figure 1). We used our knowledge of the region, topographic maps, aerial photography, and landcover data from Illinois State Geological Survey (www.isgs.uiuc.edu) and Kentucky Geography Network (kygeonet.ky.gov) to locate suitable breeding habitat within each survey area. We used ArcMap 9.1 (ESRI 2005) to estimate the proportion of total suitable habitat (km^2) surveyed.

In each of the two years, we broadcasted male songs to survey for banded recruits within appropriate breeding habitat. At approximately 75-m intervals throughout appropriate habitat, songs were played for one minute or until an individual approached and was identified. We used binoculars to observe the legs of responsive adults to determine if they were banded. We noted the location of other nearby Prothonotary Warblers (e.g. singing males and chipping females) to reduce the chance of re-counting unbanded adults. Because females are less responsive to playback, we attempted to locate and determine the banding status of females first when pairs responded to playback. Individuals with a single aluminum band were designated as banded recruits and

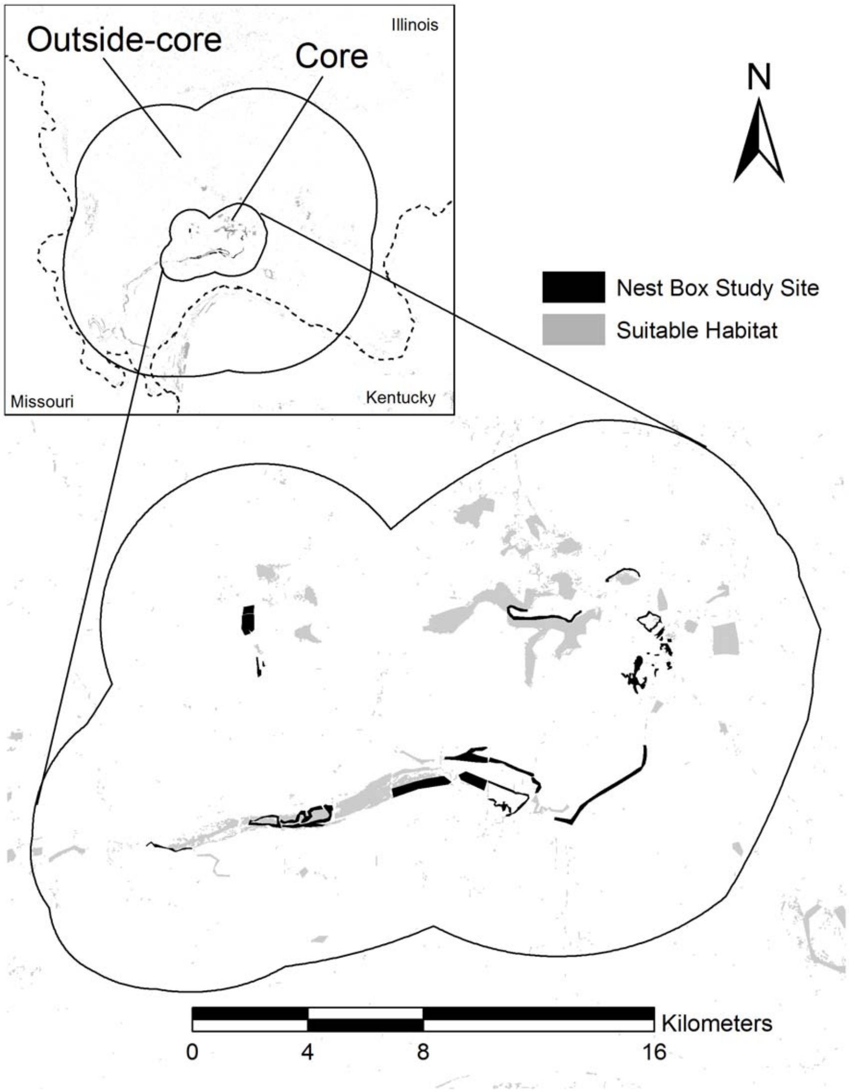

Figure 1. The entire study area depicting suitable habitat (light gray) determined by landcover data (Illinois State Geological Survey; Kentucky Geography Network) aerial photography and extensive surveys throughout the region. Black patches within core survey area indicate nest box study sites located in the Cache River watershed and dotted lines depict state boundaries.
doi:10.1371/journal.pone.0056059.g001

were subsequently captured. We placed a single yellow color-band on the left leg of banded recruits captured outside of the nest box study sites to eliminate the chance of double-counting individuals within the same survey. Banded recruits captured in the previous year, as identified by the single-yellow-plastic and aluminum band combination, were noted during the 2009 systematic surveys. In each of the two years of systematic surveys, we calculated the proportion of banded recruits within the surveyed breeding population for both the core and outside-core areas. Any one-year-old banded recruits recaptured during the systematic surveys were included in analyses of natal dispersal distances.

Detection probabilities of systematic survey. Our systematic survey could be biased if the probability of locating banded recruits varies with increased distance from the nest box area. To test for this bias, we used the systematic survey playback protocol to conduct repeated surveys at six sites (core: $n = 3$; outside-core: $n = 3$) in 2009. The survey sites were similar in size (~ 30 ha) and number of adults detected (~ 15), and were all separated by >1 km. We returned to each site on three occasions separated by at least one week. Using program MARK [25], we used occupancy modeling [26] to determine if detection probability varied between survey areas.

Distance-dependent recruitment rate

The distances between study sites and number of birds produced (and banded) per site can bias the natal dispersal distribution [27]. A distance-dependent recruitment rate (DDRR) compares the number of recruits relative to the number banded within that distance class, thereby limiting the effects of the configuration and productivity of the study sites on the resulting distribution of natal dispersal distances [20]. To calculate the DDRR we used the methods outlined in [20]. For each banded recruit, we determined the numbers of nestlings banded during the fledging year of the recruit for several distance categories relative to the fledging location of the recruit (in 2 km classes). When combined for all recruits, we calculated the average number of nestlings banded for each distance class. The observed number of recruits was then divided by the number of nestlings banded in the relative distance class to create the annual DDRR, or number of recruits observed for each nestling banded in the relevant distance class. Annual DDRRs were averaged and weighted by the number of recruits per year and are presented with standard errors. Because we were interested in corroborating the distribution of natal dispersal distances within the nest box study sites, only one-year-old banded recruits that returned to a nest box were used in this analysis.

Multistate mark-recapture analysis

We estimated first-year survival for warblers that fledged during 2004–2009 in the Cache River watershed nest box study sites. Nestlings that fledged prior to 2004 lacked measurements of nestling condition (see model covariates) and were not included in the survival analysis. To account for the possibility that recapture probability declines with increasing natal dispersal distance, we used multistate mark-recapture models [19] to incorporate the transition of individuals from fledging to one of four distance categories (<2 km, 2–4 km, 4–6 km, and >6 km) in a subsequent breeding season. Like typical Cormack-Jolly-Seber models, multistate mark-recapture allows for the estimation of survival probability (Φ) that accounts for imperfect resight/recapture probability (p). However, these models provide the added flexibility of incorporating discrete states, accounting for transitions among states (Ψ), uncertainty in state membership for occasions when an individual was not observed, and estimates of survival probability and resight/recapture probability that are specific to each state. In our case, we used distance categories as discrete states. In each individual encounter history, we classified observations as one of six states: state 1 was the initial marking prior to fledgling; states 2–5 included local recruitment into one of four dispersal distance categories; and state 6 was an 'absorbing state' representing individuals resighted or recaptured in breeding seasons after their initial recapture occasion. For example, an encounter history of 0126600 indicates the nestling was initially marked in 2005, recaptured <2 km from the nest in which it was banded (i.e. state 2) in 2006, and relocated again in 2007 and 2008. Individuals were constrained to transition from state 1 (fledgling) to one of the four distances categories (states 2–5), and to state 6 thereafter. There were no transitions among distance categories (states 2–5), to state 1, or out of state 6. We focused on resight/recapture, transition, and survival probabilities during the first year by using two age classes, first-year and adult, using a time-since-marking approach.

Model selection and goodness-of-fit. To minimize the number of models we considered, we used a three-step approach. First, we evaluated models that varied transition probability while maintaining age-dependent survival probability (i.e., first-year vs. adult), and age- and state-dependent resight/recapture probabilities. Using the top-ranked transition probability structure and age-dependent survival probability, we considered models that varied resight/recapture probabilities. In the final step, the best transition and resight/recapture probability structures were used while evaluating models that varied in survival probability. We assessed the goodness-of-fit (GOF) of our models using program U-CARE [28]. We performed multistate mark-recapture analyses in program MARK [25] and used SAS (SAS version 9.2; SAS Institute 2008) for all other analyses. Model selection was based on Akaike's Information Criterion adjusted for small sample sizes and overdispersion ($QAIC_C$) and we used model averaging to account for model-selection uncertainty and to present parameter estimates [29].

Model covariates. We evaluated the influence of four variables on survival probabilities: the number of warbler nestlings reared within the brood (range 1–6), presence of a cowbird nestmate (yes or no), fledging date (ordinal date), body condition, and an interaction between parasitism status and fledging date. We used residuals from a regression of body mass and tarsus length as an index of nestling body condition [30]. We projected the fledging date of each individual by estimating the nestling age during banding and assumed fledging at 10 days old [21]. We were unable to determine the sex of nestlings at the time of banding and thus excluded sex from the survival analysis. Variables were not highly correlated ($|r|<0.70$). Explanatory variables were considered important if their 95% confidence interval excluded zero. To ensure covariate effects were not generated by variation in detectability, we explored models incorporating the same variables as covariates for resight/recapture probability. We present all parameter estimates with ±1 standard error (SE) and survival estimates are derived from model averaging.

This study was carried out in strict accordance with the recommendations in the Guidelines to the Use of Wild Birds in Research (Available: http://www.nmnh.si.edu/BIRDNET). Research was approved by the University of Illinois Institutional Animal Care and Use Committee (Permit Numbers: 04092 and 10173), the U.S. Fish and Wildlife Service (Permit Number: MB815400-0), and the U.S. Geological Survey (Banding Permit Number: 06507).

Results

Natal dispersal distance distribution

Of the 9,289 nestlings banded prior to fledging during 1995–2009, 429 one-year-old banded recruits were captured and 250 banded recruits were first captured when they were two years old or older (total = 679, 7.3%). The median natal dispersal distance of one-year-old banded recruits ($n = 429$) did not differ between the sexes (U-test, $z = 0.78$, d.f. = 1, $P = 0.43$; Figure 2A), therefore we pooled across sex to derive the distribution of natal dispersal distances. The overall median dispersal distance was 1.42 km and the distribution of all natal dispersal distances was skewed and leptokurtic (skewness = 2.68; kurtosis = 9.00). Similarly, the mean DDRR was greatest within the <2 km distance class (0.14), and decreased with increasing distances (Figure 2B) reflecting a pattern of short-distance natal dispersal (see Figure 1d in [20]). If the pattern of natal dispersal was in fact random or long-distance in this population, the DDRR would have been either a flat or negatively-skewed curve, respectively, across distance classes.

Systematic survey for banded recruits off nest box study sites

Approximately 89% of all resighted banded recruits located off the nest box study sites during 2008 and 2009 ($n = 75$) were recaptured and identified. Although a greater amount of suitable habitat occupies the outside-core (25.5 km^2) versus core survey areas (9.65 km^2), we surveyed approximately 81% of suitable habitat and there was no significant difference in the proportion of suitable habit surveyed between each survey area ($\chi^2 = 0.33$, d.f. = 1, $P = 0.56$). More adults were examined in the outside core (2008, $n = 717$; 2009, n = 968) than within the core survey area (2008, $n = 477$; 2009, $n = 473$). The proportion of surveyed adult warblers that were banded recruits was significantly greater within the core survey area (10%) than the outside-core area (0.1%) ($\chi^2 = 156.80$, d.f. = 1, $P<0.001$). We failed to detect a significant year effect on the proportion of observed banded recruits in either survey area (core; $\chi^2 = 1.43$, d.f. = 1, $P = 0.23$, outside-core; $\chi^2 = 2.70$, d.f. = 1, $P = 0.10$). Only two banded recruits were detected in the outside-core survey area; both individuals were

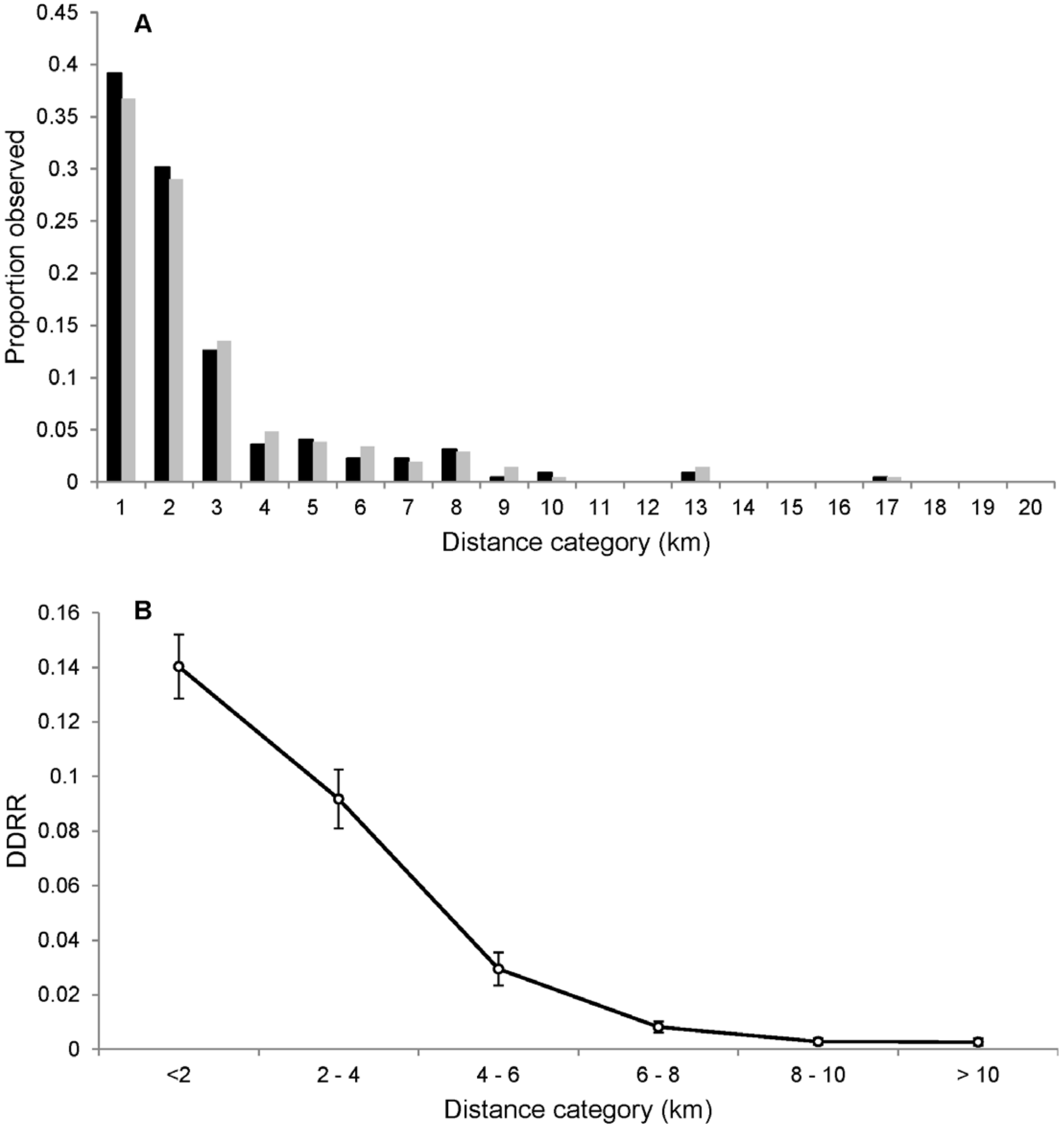

Figure 2. The distribution of natal dispersal distances for one-year-old Prothonotary Warblers in southern Illinois, fledging during 1995–2009 and recaptured on nest box study sites and within the systematic survey area. (A) The observed natal dispersal distance distribution for 222 female (black) and 207 male (gray) and (B) the distribution of observed natal dispersal distances relative to the number banded in that distance class (DDRR). Mean weighted DDRR and SEs for individuals banded prior to fledging are presented.
doi:10.1371/journal.pone.0056059.g002

observed separately ~5.25 km from the nearest nest box study site. Within the core survey area, more males (2008, $n = 400$; 2009, $n = 407$) were observed than females (2008, $n = 77$; 2009, $n = 66$), yet the proportion of surveyed birds that were banded recruits did not differ between the sexes (males = 10.7%, females = 10.4%, $\chi^2 = 0.10$, d.f. = 1, $P = 0.75$).

Detection probabilities of systematic survey. Our best supported occupancy model indicated that the detection probability of banded recruits averaged 0.89 (95% C.I. = 0.49–0.98) and did not differ between the core and outside-core survey areas. Furthermore, the relatively high estimate of detection probability of banded recruits (0.89) supports a single visit to each patch of suitable habitat was sufficient to locate most banded recruits and to allow for comparisons between core and non-core areas.

First-year survival

We analyzed the encounter histories of 6,093 individuals banded as nestlings (2004–2009), of which, 418 individuals were recaptured in a subsequent year. Although we were unable to determine sex prior to fledging, similar numbers of males ($n = 212$) and females ($n = 206$) were recaptured. The test for GOF indicated some lack of fit between the data and the JollyMove (JMV) model ($\chi^2 = 23.44$, d.f. = 14, $P = 0.05$). This lack of fit was caused by lower numbers of resights or recaptures in the following year ($\chi^2 = 16.05$, d.f. = 3, $P = 0.001$) which was confirmed by running the GOF test while suppressing the first encounter for each individual ($\chi^2 = 7.03$, d.f. = 12, $P = 0.86$). Consequently, we proceeded with fitting models with a time-since-marking structure that incorporated different survival and resight/recapture probabilities between the first and subsequent recapture periods. To reduce potential effects of overdispersion, we incorporated an estimated variance inflation factor ($\hat{c} = 1.67$) based on the sum of

Table 1. Model selection to estimate first-year apparent survival for Prothonotary Warblers, *Protonotaria citrea*, in southern Illinois, USA, fledging during 2004–2009.

No.	Φ	$QAIC_C$	$\Delta QAIC_C$	w_i	K
Models without effect of cowbird parasitism on first-year apparent survival					
1	Φ_{date}	4265.01	5.48	0.01	15
2	$\Phi_{date+cond}$	4265.44	5.91	0.01	16
3	$\Phi_{date+host\#}$	4266.34	6.81	0.00	16
4	$\Phi_{host\#}$	4296.37	36.84	0.00	15
5	Φ	4299.40	39.88	0.00	14
6	Φ_{cond}	4299.62	40.01	0.00	15
7	Φ_{year}	4303.56	44.04	0.00	19
Modeling the effect of cowbird parasitism on first-year apparent survival					
8	$\Phi_{(noBHCO=BHCO)+date}$	4259.53	0.00	0.23	16
9	$\Phi_{(noBHCO=BHCO)+date+cond}$	4259.99	0.47	0.18	17
10	$\Phi_{(noBHCO+date)\neq(BHCO)}$	4260.13	0.60	0.17	16
11	$\Phi_{[(noBHCO+date)\neq(BHCO)]+cond}$	4260.50	0.97	0.14	17
12	$\Phi_{(noBHCO+date)\neq(BHCO+date)}$	4261.30	1.78	0.09	17
13	$\Phi_{[(noBHCO+date\neq(BHCO+date)]+cond}$	4261.74	2.22	0.07	18
14	$\Phi_{(noBHCO=BHCO)+date+cond+host\#}$	4261.92	2.39	0.07	18
15	$\Phi_{(noBHCO=BHCO)}$	4297.73	38.21	0.00	15
16	$\Phi_{(noBHCO=BHCO)+year}$	4306.83	47.30	0.00	24

Φ, apparent survival; $QAIC_C$, quasi-likelihood Akaike's information criterion corrected for small sample size; w_i, Akaike's model weights; K, number of parameters; *date*, ordinal fledging date; *BHCO*, reared with cowbird nestmate; *noBHCO*, absence of cowbird nestmate; *cond*, nestling body condition; *host#*, number of warbler nestmates within brood; =, indicates no interaction between terms; ≠, indicates an interaction between terms; year, annual variation; (.), indicates a constant for parameter.

doi:10.1371/journal.pone.0056059.t001

the GOF tests in U-CARE (calculated as χ^2 divided by the degrees of freedom).

Transition probabilities. Models with a two-stage structure (State 1→States 2–5, and States 2–5→State 6) had much greater support than the constant model ($\Delta\ QAIC_C = 139.62$). There was little support for annual variation in transition probabilities ($\Delta\ QAIC_C = 5.87$). The transition model with the greatest support ($w_i = 0.99$) incorporated variation from state 1 to each distance-specific state (2–5), while the transitions between states 2–5 to the 'absorbing' state 6 were held constant (Table S1). Transition probabilities decreased dramatically with distance, with the highest probability of local recruitment within the <2 km distance category (0.68 ± 0.02; Figure S1). This transition structure was used in subsequent modeling of recapture probabilities and survival rates (Table S1).

Recapture probabilities. Contrary to expectations, recapture probabilities from this study did not decrease with increasing dispersal distance. In a model that included variation in first-year recapture probabilities among distance categories ($p_{age,dist}$), recapture probabilities declined slightly from the first distance category (<2 km; 0.45 ± 0.03) to the second (2–4 km; 0.36 ± 0.07), but increased within state 3 (4–6 km; 0.53 ± 0.14). Because distance-related first-year recapture probabilities were not supported ($w_i < 0.01$), we only used models incorporating annual variation for subsequent analyses (Table S2). The top-ranked recapture model incorporated an effect of year on first-year recapture probabilities and constant probability for ages >1 year old ($w_i = 0.98$; Table S2). Recapture probability for first-year warblers varied between 0.56 (±0.06) and 0.28 (±0.05) among years.

Survival probabilities. Incorporating the top-ranked transition and recapture structures, models that included two age-classes in survival probability estimates were better supported than a constant model ($\Delta QAIC_C = 39.88$). Annual variation in first-year survival probability was not supported when compared to the age-class model (Table 1). Thus, individual covariates were applied to a two age-class model that included time-constant survival probability estimates.

First-year survival estimates varied as a function of fledging date and parasitism status (Table 1). The top ranked model (Model 8; Table 1), included similar linear trends for the effect of fledging date on individuals reared with a cowbird nestmate (BHCO) and without (noBHCO). Overall, all models <10 $\Delta QAIC_C$ included fledging date, and model averaged estimates of first-year survival declined with increasing fledging dates both for individuals reared with and without a cowbird nestmate (Figure 3). Similarly, while holding other covariates at mean observed values, model averaged survival estimates were nearly 2 times greater for individuals reared without cowbirds (0.11 ± 0.01) than reared with a cowbird nestmate (0.06 ± 0.01) (Figure 3). An interaction between the effects of fledging date and cowbird parasitism on first-year survival were marginally supported. The model fit was slightly improved by removing the effect of date for group BHCO (Table 1; Models 10 and 11) and the predicted model-averaged estimates indicated that first-year survival decreased with fledging date less sharply for individuals reared with a cowbird nestmate (BHCO) than those without (noBHCO) (Figure 3).

Variation in nestling body condition (*cond*) was only marginally supported to influence first-year survival. Despite a model incorporating condition having nearly equal support to the top-

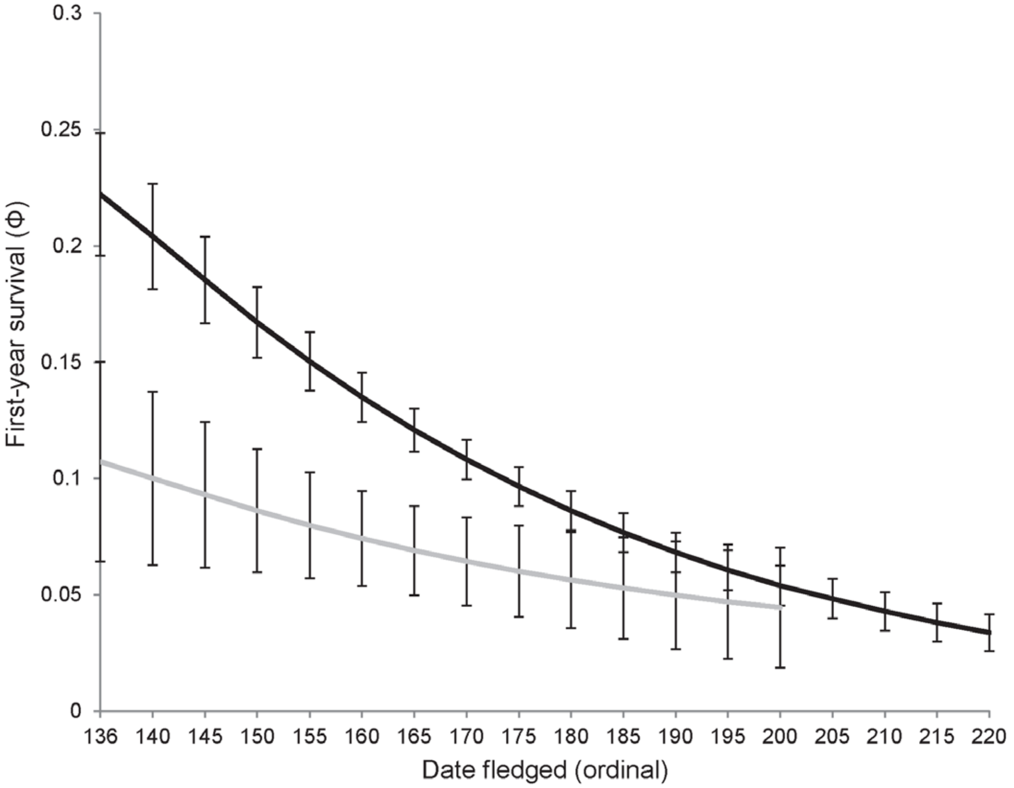

Figure 3. The relationship between fledge date (ordinal fledging date 136 = 15 May) and first-year survival for Prothonotary Warblers. Model averaged estimates (mean ± 1SE) of warblers reared with Brown-headed Cowbirds (grey line) and in the absence of cowbirds (black line) in southern Illinois, USA, fledging during 2004–2009 are presented. All other variables were held at mean observed values.
doi:10.1371/journal.pone.0056059.g003

ranked model (Model 9; $\Delta QAIC_C = 0.47$), the 95% CI overlapped zero ($\beta_{cond} = 0.09$, 95% CI: -0.05 to 0.23) and the model including this covariate alone (Model 6) was not supported. The effect of number of warblers within the brood (*host#*) on first-year survival was unimportant ($\beta_{host\#} = 0.01$, 95% CI: -0.14 to 0.16). When the survival covariate structures were interchanged with the recapture probabilities, $QAIC_C$ decreased by >2, suggesting that variation in survival estimates was not being driven by the effects of explanatory variables on recapture probabilities.

Discussion

In lieu of reliable estimates of first-year survival, population modelers have used theoretical values thought to represent adequate population-level replacement rates, such as one-half of adult survival, or ~0.30 ([13,14] reviewed by [12]). In contrast, we found both the mean (0.11 ± 0.01) and maximum (early fledged; 0.22 ± 0.03) first-year survival estimates for non-parasitized Prothonotary Warblers to be much less than the expected rate of first-year survival for a migratory passerine.

The Cache River nest box study system provided a rare opportunity to investigate natal dispersal and ultimately first-year survival for a migratory passerine, as the nest boxes allowed for a large sample size and the habitat specificity of the warblers enabled us to focus our search for banded recruits. While exciting new statistical methods are being developed to account for the rate of permanent emigration [9,31], the multistate mark-recapture modeling allowed for variable resight/recapture probabilities as a function of distance and minimized the traditional biases inherent to these types of studies. Our systematic surveys for natal dispersal events outside of the nest box study system, distribution of natal dispersal distances, and the distance-dependent recruitment rate all suggested that permanent emigration was relatively rare in our study system. Survival would be underestimated if long-distance natal dispersal (i.e. outside of systematic survey area) were common in this population. However, Winkler et al. [32] summarized data from one of the largest study areas and sample sizes for a Neotropical migrant to date and also found that long-distance natal dispersal occurs rarely (1.3% of observed dispersal events at 50–200 km) while the majority of first-year Tree Swallows (*Tachycineta bicolor*) returned to breed within 10 km (median = 2.8 km) of their natal origin. Although Prothonotary Warblers dispersing (i.e. permanently emigrating) off the nest box sites were detected in our systematic surveys, survival estimates and resight/recapture probabilities during the years of systematic surveys did not increase. Even though apparent survival estimates always represent a minimum value for the true estimate, we believe that by accounting for dispersal and using multistate mark-recapture models that incorporate factors influencing survival and resight/recapture probability, including distance, we calculated robust estimates of first-year survival.

For populations with low juvenile survival, relatively high adult survival or fecundity would be required to maintain population stability. As adults tend to disperse between years after experiencing nesting failure, adult survival estimates in migratory passerines (i.e. 0.60) would likely be increased with the incorporation of reproductive performance [18]. For example, experimental manipulations of reproductive success randomly assigned to Prothonotary Warblers led to the discovery that adult return rates in double-brooded individuals is approximately 0.80 [33]. As a return rate is a minimum estimate of survival, adult survival for Prothonotary Warblers is likely greater than 0.80 and low juvenile survival (i.e. 0.11) may be offset by very high adult survival. Using these survival rates (0.11 for juveniles and 0.80 for adults) and a simple population model [$\lambda = \text{adult survival} + (\text{fecundity} \times \text{juvenile survival})$], a fecundity value of 1.82 would be necessary to achieve population stability (i.e. $\lambda = 1.00$). Indeed, during our many years of working in this study system, fecundity values have often met or exceeded the value necessary for populations to maintain themselves in the watershed [24,34,35]. In addition, the relatively short median natal dispersal distances (e.g. <2 km) we observed strongly suggests that local conservation and habitat management efforts to increase nesting success of this species will have positive effects on local breeding populations.

Juvenile survival estimates in migratory species are exceedingly rare, but a few studies have projected first-year survival estimates by combining post-fledging survival rates with survival estimates documented within the breeding and non-breeding areas [36] and also reported values well below 0.30: between 0.18 and 0.24 (Lark Bunting, *Calamospiza melanocorys*) [8]; and between 0.15 and 0.18 (Black-throated Blue Warbler, *Setophaga caerulescens* [37]). While relatively low juvenile survival may be representative of many migratory songbird populations, other recent estimates have indicated that juvenile survival is variable and may reflect differences in life history traits [1,3,38,39]. For example, juvenile survival estimates in two aerial insectivores were more than twice as high as the estimate found for Prothonotary Warblers (Purple Martin, *Progne subis* = 0.27 [40]; Eastern Kingbird, *Tyrannus tyrannus* = 0.29 [41]) and may reflect differences in how these species experience the first weeks of the post-fledging period. Purple Martins are fully capable of extended flight when they fledge and spend much of the time foraging while in flight [40], and Eastern Kingbirds can sustain short flights during the early part of the post-fledging period [42]; in each case resulting in very low post-fledging mortality rates. In contrast, recently-fledged Prothonotary Warblers are poor flyers, not very mobile, and still highly dependent on their parents, possibly making them more vulnerable to predators during this period. Our estimate of low juvenile survival (i.e. 0.11) in Prothonotary Warblers may not be generalizable to all migratory passerines, but may represent what juvenile survival is in other forest-dwelling Neotropical migrants. Additional studies that combine intensive efforts to locate returned juveniles over a large area with new and emerging modeling and analysis techniques to generate estimates of juvenile survival in other species will clarify whether our value of 0.11 is more an exception or a general rule.

Considerable variation in first-year survival rates were observed with the inclusion of biotic factors into our survival models. The probability of first-year apparent survival was on average 40% lower for those reared with a parasitic cowbird nestmate than for those reared with only host nestmates. Despite fledging from the nest, the inability of host young to adequately compete with brood parasites for food during the nestling stage [43,44] may increase the probability of mortality post fledging. However, our measurements of body condition for nestlings did not appear to explain the observed decrease in survival, regardless of parasitism status. There may be other negative effects of cowbirds not measured in this study (e.g. reduced immune function [45]) that reduce survival rates for individuals reared with cowbird nestmates. In addition, brood parasites likely continue to disproportionally procure resources during the post-fledging period, potentially reducing body condition further and thereby reducing survival prior to independence for hosts [46,47]. Competition for food between host and parasitic fledglings could leave host fledglings in a weakened condition and less able to escape from predators or cause them to increase their begging only to attract more predators [48].

The probability of first-year survival decreasing with later fledging dates (i.e. a seasonal effect) has been reported in populations of resident species (reviewed in [49]), and recently in migratory passerines [40,50]. First-year survival estimates for non-parasitized warblers decreased from 0.22 (±0.02) to 0.03 (±0.03) for fledge dates across the breeding season, with a substantial reduction during the first month (0.12). Parental quality and seasonal variation in ecological factors (e.g. food limitation, parasites, predation), two common hypotheses explaining temporal variation in reproductive performance [49], may also explain why first-year survival rates decreased with later fledging dates. In migratory birds, adults of 'high quality' are thought to arrive on the breeding grounds earlier and subsequently initiate breeding prior to individuals of 'lower' quality [51]. However, the parental quality hypothesis alone fails to explain the dramatic decline in first-year survival with increasing fledging dates found in this study. A majority (>65%) of the adult females fledging offspring late in the season were known to have also bred earlier (April and May) within the same year. If it were simply parental quality driving the seasonal decline, first-year survival probabilities in late-fledged birds would likely be much greater because most 'high quality' individuals (i.e. early breeding birds) bred a second time. As a substantial portion of first-year mortality likely occurs during the post-fledging stage (reviewed in [12]), the influence of food availability [8] or intensity of predation [48] may increase as the breeding season progresses, thus reducing survival of fledglings prior to migration. Finally, lacking the ability to use previous migratory movements for navigation, juveniles may incur a greater risk of mortality during fall migration than adults [39]. Individuals that fledge earlier in the breeding season may benefit from having additional time to adequately prepare for migration (e.g. fat reserves), thereby increasing the probability of successfully reaching the wintering grounds [50].

The very low juvenile survival found in this population suggests that mortality rates during the first year of life for many Neotropical migrants are potentially greater than previously thought. Brood parasitism and timing of reproduction are important effects on first-year survival and, subsequently, provide insights into potential areas of vulnerability in populations of conservation concern. Estimates used in past population models (e.g. one-half of adult survival) are unlikely to reflect first-year survival for all migratory passerine populations, and future population models should incorporate a range of first-year and adult survival rates. Furthermore, current estimates of adult survival in migratory songbirds are likely biased low and future research should incorporate reproductive success into survival models to account for permanent emigration after reproductive failure [17]. In study systems where banded recruits cannot be searched for systematically, juvenile survival could be estimated by incorporating the dispersal distribution within a mathematical framework to determine the rate of permanent emigration [8,30]. Increasing the accuracy of age-specific survival estimates is necessary to enhance our understanding of population dynamics, tradeoffs in reproduction and the evolution of avian life histories.

Supporting Information

Figure S1 Probability (mean ± 1 SE) of transition between fledging and four distance categories for Prothonotary Warblers in southern Illinois, USA, 2004–2010.
(TIFF)

Table S1 Model selection to estimate transition probabilities for Prothonotary Warblers, *Protonotaria citrea*, in southern Illinois, USA, 2004–10.
(DOCX)

Table S2 Model selection to estimate recapture probabilities for Prothonotary Warblers, *Protonotaria citrea*, in southern Illinois, USA, 2004–10.
(DOCX)

Acknowledgments

We thank A. Albores, N. Davros and the numerous field assistants who helped collect warbler data over several years. We are grateful for the discussions and comments from J. Brawn, P. Weatherhead, Scott Sillett, John Faaborg, and University of Illinois Bird lab. Staff from the Illinois Natural History Survey, Cypress Creek National Wildlife Refuge and Cache River State Natural Area provided logistical support.

Author Contributions

Conceived and designed the experiments: MIM JPH TJB WMS. Performed the experiments: MIM JPH WMS. Analyzed the data: MIM TJB. Contributed reagents/materials/analysis tools: JPH WMS. Wrote the paper: MIM JPH TJB WMS.

References

1. Sæther BE (1988) Pattern of covariation between life-history traits of European birds. Nature 331: 616–617.
2. Clark ME, Martin TE (2007) Modeling tradeoffs in avian life history traits and consequences for population growth. Ecological Modelling 209: 110–120.
3. Tarwater CE, Ricklefs RE, Maddox JD, Brawn JD (2011) Pre-reproductive survival in a tropical bird and its implications for avian life histories. Ecology 92: 1271–1281.
4. Robinson RA, Green RE, Baillie SR, Peach WJ, Thomson DL (2004) Demographic mechanisms of the population decline of the song thrush *Turdus philomelos* in Britain. Journal of Animal Ecology 73: 670–682.
5. Sim IMW, Rebecca GW, Ludwig SC, Grant MC, Reid JM (2011) Characterizing demographic variation and contributions to population growth rate in a declining population. Journal of Animal Ecology 80: 159–170.
6. Schaub M, Reichlin TS, Abadi F, Kery M, Jenni L, et al. (2012) The demographic drivers of local population dynamics in two rare migratory birds. Oecologia 168: 97–108.
7. Anders AD, Faaborg J, Thompson FR (1998) Postfledging dispersal, habitat use, and home-range size of juvenile wood thrushes. Auk 115: 349–358.
8. Adams AAY, Skagen SK, Savidge JA (2006) Modeling post-fledging survival of lark buntings in response to ecological and biological factors. Ecology 87: 178–188.
9. Cooper CB, Daniels SJ, Walters JR (2008) Can we improve estimates of juvenile dispersal distance and survival? Ecology 89: 3349–3361.
10. Lebreton JD, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case-studies. Ecological Monographs 62: 67–118.
11. Weatherhead PJ, Forbes MRL (1994) Natal philopatry in passerine birds: genetic or ecological influences? Behavioral Ecology 5: 426–433.
12. Faaborg J, Holmes RT, Anders AD, Bildstein KL, Dugger KM, et al. (2010) Recent advances in understanding migration systems of New World land birds. Ecological Monographs 80: 3–48.
13. Ricklefs RE (1973) Fecundity, mortality, and avian demography. In Farner DS, editor. Breeding biology of birds. National Academy of Science: Washington, D.C. 366–435 p.
14. Donovan TM, Thompson FR, Faaborg J, Probst JR (1995) Reproductive success of migratory birds in habitat sources and sinks. Conservation Biology 9: 1380–1395.
15. Paradis E, Baillie SR, Sutherland WJ, Gregory RD (1998) Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology 67: 518–536.
16. Tittler R, Villard MA, Fahrig L (2009) How far do songbirds disperse? Ecography 32: 1051–1061.
17. Koenig WD, VanVuren D, Hooge PN (1996) Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution 11: 514–517.
18. Anders AD, Marshall MR (2005) Increasing the accuracy of productivity and survival estimates in assessing landbird population status. Conservation Biology 19: 66–74.
19. Lebreton JD, Nichols JD, Barker RJ, Pradel R, Spendelow JA (2009) Modeling individual animal histories with multistate capture-recapture models. Advances in Ecological Research, Vol 41. San Diego: Elsevier Academic Press Inc. pp. 87–173.
20. van Noordwijk AJ (2011) Measuring dispersal as distance-dependent recruitment rates: testing the performance of DDRR on simulated data. Journal of Ornithology 152: 239–249.
21. Petit LJ (1999) Prothonotary warbler (*Prothonotaria citrea*). In Poole A, Gill F. editors. The Birds of North America. Philadelphia: The Birds of North America Inc.
22. Hoover JP (2003) Experiments and observations of prothonotary warblers indicate a lack of adaptive responses to brood parasitism. Animal Behaviour 65: 935–944.
23. Hoover JP (2003) Multiple effects of brood parasitism reduce the reproductive success of prothonotary warblers, *Protonotaria citrea*. Animal Behaviour 65: 923–934.
24. Hoover JP (2001) An experimental study of the behavioural responses to nest predation and brood parasitism in a migratory songbird [Ph.D.]. Urbana: University of Illinois.
25. White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. Bird Study 46: 120–139.
26. MacKenzie DI, Nichols JD, Lachman GB, Droege S, Royle JA, et al. (2002) Estimating site occupancy rates when detection probabilities are less than one. Ecology 83: 2248–2255.
27. vanNoordwijk AJ (1995) On bias due to observer distribution in the analysis of data on natal dispersal in birds. Journal of Applied Statistics 22: 683–694.
28. Choquet R, Lebreton JD, Gimenez O, Reboulet AM, Pradel R (2009) U-CARE: Utilities for performing goodness of fit tests and manipulating capture-recapture data. Ecography 32: 1071–1074.
29. Burnham KP, Anderson DR (2002) Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach. New York: Springer-Verlag.
30. Schulte-Hostedde AI, Zinner B, Millar JS, Hickling GJ (2005) Restitution of mass-size residuals: Validating body condition indices. Ecology 86: 155–163.
31. Gilroy JJ, Virzi T, Boulton RL, Lockwood JL (2012) A new approach to the “apparent survival” problem: estimating true survival rates from mark–recapture studies. Ecology 93: 1509–1516.
32. Winkler DW, Wrege PH, Allen PE, Kast TL, Senesac P, et al. (2005) The natal dispersal of tree swallows in a continuous mainland environment. Journal of Animal Ecology 74: 1080–1090.
33. Hoover JP (2003) Decision rules for site fidelity in a migratory bird, the prothonotary warbler. Ecology 84: 416–430.
34. Hoover JP (2009) Effects of hydrologic restoration on birds breeding in forested wetlands. Wetlands 29: 563–573.
35. Hoover JP (2009) Prothonotary Warblers as indicators of hydrological conditions in bottomland forests. In: Rich TD, Arizmendi C, Demarest DW, and Thompson C, editors. pp. 128–137. Tundra to Tropics: proceedings of the fourth International Partners in Flight Conference.Partners in Flight, McAllen, Tex.
36. Sillett TS, Holmes RT (2002) Variation in survivorship of a migratory songbird throughout its annual cycle. Journal of Animal Ecology 71: 296–308.
37. Reilly JR, Reilly RJ (2009) Bet-hedging and the orientation of juvenile passerines in fall migration. Journal of Animal Ecology 78: 990–1001.
38. Stearns SC (1992) The evolution of life histories. Oxford: Oxford University Press. 264 p.
39. Martin TE (1995) Avian life history evolution in relation to nest sites, nest predation, and food. Ecological Monographs 65: 101–127.
40. Tarof SA, Kramer PM, Hill JR, Tautin J, Stutchbury BJM (2011) Brood size and late breeding are negatively related to juvenile survival in a Neotropical migratory songbird. Auk 128: 716–725.
41. Redmond LJ, Murphy MT (2012) Using complementary approaches to estimate survival of juvenile and adult eastern kingbirds. Journal of Field Ornithology 83: 247–259.
42. Murphy MT (1983) Ecological aspects of the reproductive-biology of eastern kingbirds: geographic comparisons. Ecology 64: 914–928.
43. Lichtenstein G, Sealy SG (1998) Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. Proceedings of the Royal Society of London Series B-Biological Sciences 265: 249–254.
44. Kilner RM, Madden JR, Hauber ME (2004) Brood parasitic cowbird nestlings use host young to procure resources. Science 305: 877–879.
45. Cichon M, Dubiec A (2005) Cell-mediated immunity predicts the probability of local recruitment in nestling blue tits. Journal of Evolutionary Biology 18: 962–966.
46. Ridley AR, Thompson AM (2012) The effect of jacobin cuckoo *Clamator jacobinus* parasitism on the body mass and survival of young in a new host species. Ibis 154: 195–199.
47. Peterson SM, Streby HM, Andersen DE (2012) Effects of parasitism by brown-headed cowbirds may persist into post-fledging. Wilson Journal of Ornithology 124: 179–183.

48. Götmark F (2002) Predation by sparrowhawks favours early breeding and small broods in great tits. Oecologia 130: 25–32.
49. Verhulst S, Nilsson JA (2008) The timing of birds' breeding seasons: a review of experiments that manipulated timing of breeding. Philosophical Transactions of the Royal Society B-Biological Sciences 363: 399–410.
50. Mitchell GW, Guglielmo CG, Wheelwright NT, Freeman-Gallant CR, Norris DR (2011) Early life events carry over to influence pre-migratory condition in a free-living songbird. Plos One 6: e28838.
51. Møller AP, De Lope F, Saino N (2004) Parasitism, immunity, and arrival date in a migratory bird, the barn swallow. Ecology 85: 206–219.