

NATAL DISPERSAL AND FIRST-YEAR SURVIVAL
IN A NEOTROPICAL MIGRATORY SONGBIRD

BY

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THESIS

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Abstract

Juvenile survival is among the most important demographic parameters driving population dynamics in birds. However, because first-year (i.e. 1-year-old) migratory passerines are thought to return to breed at great distances from their natal location, the factors that influence first-year survival have not been thoroughly investigated. To examine the factors that affect first-year survival, I determined the distribution of natal dispersal distances in Prothonotary Warblers (*Protonotaria citrea*) breeding within a nest box study system covering a large area. Surveys outside the nest box study system (up to 30 km in all directions) supported the legitimacy of the dispersal pattern calculated from the nest box study. By incorporating natal dispersal distance into a multi-state model framework, I accounted for the potential confounding effect of dispersal distance on recapture probabilities. Using this model framework, I investigated the effects of season, presence of a cowbird nestmate, brood size, and nestling body condition on the first-year survival probabilities. To date, this is the first study to document that both fledging date and the presence of a cowbird nestmate affect first-year survival in a migratory songbird.

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CHAPTER 1

Short-distance natal dispersal in a Neotropical migratory songbird

1.1 Abstract

Although we currently understand remarkably little about the natal dispersal patterns of birds, it is assumed that most long-distance migratory passerines breed far from natal locations. Return rates lower than expected may reflect inherent issues associated with studying migratory birds (e.g. limited study areas, few marked individuals, vast available habitat) rather than actual natal dispersal events over long distances. From 1995-2008, I banded nestling prothonotary warblers (*Protonotaria citrea*) (n = 7926) in southern Illinois as part of a long-term study using nest boxes. I then recaptured those nestlings that came back to the study sites to breed (i.e. banded recruits). Natal dispersal distances did not differ between males and females and mean and median distances for all individuals combined were 2200 m and 1420 m, respectively. To determine whether natal dispersal distances calculated from this nest-box study were a result of limitations associated with the size of the study system, I expanded the search for banded recruits and surveyed warblers in the majority (81%) of total available breeding habitat within a 30-km buffer surrounding all nest box study sites during the breeding seasons of 2008 and 2009. I compared the proportion of recruits observed within the sample of breeding adults surveyed on non-nest box sites within the core study area (5-km buffer surrounding nest boxes) and outside the core (from 5 km to 30 km surrounding nest boxes). The proportions of recruits observed within the core (9% in 2008 and 7% in 2009) were significantly greater than the proportions of recruits outside the core (< 1% in 2008 and 0% in 2009). Based on systematic surveys outside the core study area and the observed natal dispersal distribution, I conclude that a vast majority of prothonotary warblers return to breed near their natal origins.

Keywords: Juvenile survival, Local recruitment, Philopatry, Prothonotary warbler

1.2 Introduction

The accumulation of individual natal dispersal events impacts nearly every aspect of population ecology including genetic structure, demography, and behavioral adaptations (Clobert 2001; Greenwood and Harvey 1982). However, the difficulties associated with accurately characterizing dispersal patterns, especially in vagile species, have made natal dispersal one of the least understood life history traits (Clobert 2001). Natal dispersal distance, the straight-line distance between birth and breeding sites, is often variable within a population as some juveniles disperse far while others subsequently breed near their natal origin. Inherent to studies in open populations, the inability to differentiate between permanent emigration and mortality directly impacts the accuracy of survival estimates (Cooper et al. 2008). A better understanding of natal dispersal patterns, particularly in Neotropical migratory birds, is therefore critical to more accurately model population dynamics and assess conservation efforts for migratory songbirds breeding in fragmented landscapes (Faaborg et al. 2010a).

The remarkable mobility of birds has created challenges to accurately document natal dispersal. Natal dispersal distances are thought to vary based on differences in sex (Clarke et al. 1997; Greenwood 1980) or body mass (Sutherland et al. 2000), but there is remarkably little known about the distributions of natal dispersal distances for most migratory birds. Past studies have generally employed mark-recapture techniques to investigate broad-scale patterns of natal dispersal. Studies investigating the distribution of distances moved between the natal and first breeding locations typically document a sharp decrease in the frequency of observations with increased distance. Typically, measurements of natal dispersal are reported in units of distance or as the proportion of banded juveniles that breed within the study area where they were produced (i.e. natal philopatry). Relatively short natal dispersal distances may be common in systems with limited dispersal opportunities including colonial species (Brown and Brown 1992), cooperative breeders (Stith 1996), and resident (Weatherhead and Forbes

1994; Plissner and Gowaty 1996) and island populations (Weatherhead and Forbes 1994; Wheelwright and Mauck 1998) of Neotropical passerines.

Reported patterns of short-distance natal dispersal in migratory birds breeding within continuous, intact habitats (DiQuinzio et al. 2001; Forschler et al. 2010; Payne 1991; Sedgwick 2004) may, however, reflect limitations associated with the size of the study area. The probability of detecting a recruit outside of the study area is essentially zero, thus, the proportion of dispersal events observed depends on the relationship between actual dispersal distances and the size of the study area (Koenig et al. 1996). A potential result of unknown numbers of undetected recruits returning to breed off the study plot (Lambrechts et al. 1999) is that typically less than 5% of hatchlings banded prior to fledging are found in subsequent breeding seasons (Weatherhead and Forbes 1994). There is support for migratory passerines to have greater median and maximum natal dispersal distances than resident populations (Paradis et al. 1998; Sutherland et al. 2000). It remains unclear whether the observed low return rate (i.e. resembling long-distance dispersal) of juveniles banded in populations of migratory birds is caused by low survival and/or increased dispersal.

In contrast to residents, migrant birds spend only a limited portion of their annual cycle near the breeding area, thereby adding to the difficulty of precisely identifying natal dispersal patterns in migrants. If migratory species do, in fact, tend to disperse farther, then sampling bias created by limited study areas may be much more pronounced in migrants than in residents. Because the ability to detect an individual dispersal event is restricted by the size of the study area and detection probabilities tend to decrease with distance, natal dispersal distributions are typically biased towards short-distances (Koenig et al. 1996). Additional biases may result if the proportion of observer effort is greatest near the banding location (i.e. natal location) (vanNoordwijk 1995). An additional challenge of studies of natal

dispersal in migratory birds has been the failure to gain adequate sample sizes of banded juveniles as a result of limitations in locating and monitoring nests.

Acquiring relatively unbiased data with adequate sample sizes is typically difficult or impossible in direct mark-recapture studies, resulting in the development of other techniques to indirectly estimate natal dispersal patterns in Neotropical migratory songbirds. Stable-hydrogen isotope ratios in feathers have been used to estimate the geographic location where feathers are grown (Chamberlain et al. 1997) and comparisons of these ratios among one-year-old individuals have been used to infer natal dispersal distances (Studds et al. 2008). Recently, one-year time-lagged correlations in total abundance of numerous passerine species, (estimated from North American Breeding Bird Survey data) were used to infer broad-scale natal dispersal patterns (Tittler et al. 2009). Although these indirect methods indicate patterns of long-distance (> 50 km) natal dispersal in migratory species, variation in isotope ratios may reflect error due to sampling (Smith et al. 2009) and the source of time-lagged correlations in bird abundances remains to be identified. Of the direct measures used to estimate patterns of natal dispersal, radio or GPS telemetry would be among the best techniques (Koenig et al. 1996). However, due to migratory nature and small size of most Neotropical migratory passerines, current limitations in battery life eliminates the possibility of using transmitters to study natal dispersal. To directly estimate the natal dispersal distance of an individual and document the pattern of a given population, traditional banding and re-sight/recapture techniques are currently the best available technique.

It is generally thought that most juvenile Neotropical migratory passerines return to breed at locations that are relatively far from their hatch-site (Faaborg et al. 2010b) and that few juveniles are recruited back into their natal population. Actual tests of this dogma have been scarce. The combination of breeding habitat specificity, use of nest boxes, and aggressive response to song playback make the prothonotary warbler (*Prothonotaria citrea*) a good candidate species to thoroughly investigate natal

dispersal in a long-distance Neotropical migratory songbird. Acknowledging the biases caused by limited study areas, my primary objectives were to 1) document the distribution of natal dispersal distances of prothonotary warblers breeding in a nest box study system that covers a large area, and 2) extend the search for individuals that were banded as nestlings and returned (hereafter “banded recruits”) to suitable breeding habitat outside of the nest box study area to evaluate the validity of the distribution. I also determined if dispersal distances differed between the sexes, which could have potentially biased my ability to relocate the more dispersive sex.

1.3 Materials and Methods

Study area and species

The entire study area was located in southern Illinois and western Kentucky, U.S.A., covering an area of approximately 4,875 km² (Fig. 1). This large area was divided into nest box sites, core, and outside-core areas (see descriptions below). The land cover within the study area consists of approximately 9% wet forested habitat, 32% agriculture, 31% grasslands and pastures, 26% forested uplands, and 2% residential (Mankowski 1997). Prothonotary warblers are long-distance migratory passerines that winter in the Neotropics and breed throughout the eastern portion of the United States. These warblers nest near or over water in secondary cavities within forested swamps and flooded bottomland forests (Petit 1999), and will readily use nest boxes when available. Additional information about the ecology and behavior of this warbler are described in detail elsewhere (Hoover 2003; Petit 1999). To study the natal dispersal of prothonotary warblers, I used information gathered from a large (18 km east-west, 12 km north-south; Fig. 1) nest box study system located in the Cache River watershed in southern Illinois from 1996 through 2009.

Field methods

Each year, nest boxes (approximately 1500) were distributed among 20-25 study sites in a grid pattern (40-50 m spacing) within appropriate breeding habitat. Nest boxes were placed 1.7 m above ground and had 44-mm diameter openings, reflecting the natural cavities used by adult warblers (Hoover 2001). Nest boxes were monitored every 3-6 days throughout each breeding season. At each active nest, the numbers of warbler eggs and nestlings were recorded, and the fate of the nest (offspring fledged or not) was determined. Each nestling was banded prior to fledging, at 5-8 days old, with a uniquely-numbered aluminum U.S. Geological Survey band on its right leg.

Banded recruits were identified as those adults in the breeding population with a single aluminum band on the right leg. I determined the breeding location of banded recruits by their association with active nest boxes or by territorial behavior. Greater than 95% of the male and female banded recruits observed, were captured using playback with a decoy placed next to a mist-net, or while incubating. Once captured, I determined the origin of each banded recruit and determined their natal dispersal distance by measuring the straight-line distance between the birth site and the recapture (breeding) location. Nest boxes and recapture locations were recorded with a global positioning system (GPS) unit or on topographic maps, accurate to approximately 10-50 m. Because prothonotary warblers typically start breeding when they are one year old (Petit 1999), I calculated natal dispersal distances only for first-year banded recruits (i.e. one-year-old birds).

Systematic survey for banded recruits

In addition to the information collected from the nest box study sites, I conducted a systematic survey in 2008 and 2009 to locate banded recruits of all ages outside of the nest box study sites. I defined the core survey area as all suitable breeding habitat located in the interstitial areas between nest box sites and within a 5 km buffer surrounding the nest box sites (Fig. 1). Suitable breeding habitat

located from 5 km to 30 km surrounding the core survey area was defined as outside-core (Fig. 1). I used topographic maps, aerial photography, and prior knowledge to locate suitable breeding habitat within the survey areas. I used the land cover category “swamp” classified from available land cover data (Illinois State Geological Survey; Kentucky Geography Network) and ARCMAP, version 9.1, to estimate the proportion of suitable habitat surveyed within both survey areas. Because first-year recruits typically return one to two weeks later than older adults during the breeding season (Hoover 2001), I performed surveys between 15 May and 4 July each year.

In each of the two years, I broadcast territorial male songs with an mp3 player and speakers to survey for banded recruits within appropriate breeding habitat. Songs were played every 75 m for one minute or until an individual approached and was identified. With 10x binoculars, I observed the tarsi (legs) of responsive adults to determine if they were banded. During each encounter, I 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, I 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 were subsequently captured with a mist-net and decoy. I placed a single yellow color-band on the left leg of banded recruits captured outside of the nest box area 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, I 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 observed during the systematic surveys were included in analyses of natal dispersal distances.

Comparison of Detection Probabilities

Potential biases could result if the probability of locating banded recruits varies with increased distance from the nest box area. Following the systematic survey playback protocol, in 2009 I conducted repeated surveys at six sites (core: $n = 3$; outside-core: $n = 3$). The survey sites were similar in size (~ 30 ha), number of adults detected (~ 15) and were all separated by > 1 km. I returned to each site on three occasions separated by at least one week. Using program MARK (White and Burnham 1999), I used the occupancy estimation (MacKenzie et al. 2002) to determine if detection probability varies between the survey areas. Within each encounter history, '1' indicated detection of a banded recruit and '0' indicated nondetection. For example, an encounter history 011 indicates at least one banded recruit was present but missed during the first survey occasion. The model with the strongest support indicated detection probability of banded recruits did not differ between the core and outside-core survey areas (i.e. constant) and averaged 0.89 (95% C.I. = 0.49-0.98).

Statistical analysis

I used SAS, version 9.2 (SAS Institute, Cary, North Carolina) for the following statistical analyses. The Wilcoxon-Mann-Whitney U -test was used to determine if sex affected natal dispersal distance. I used a χ^2 test to compare the proportions of suitable habitat covered by the systematic surveys between the core and outside-core areas. To evaluate if recruitment of banded warbler nestlings was spatially homogenous across the landscape, I used χ^2 tests to compare the proportion of banded recruits detected in the surveyed breeding populations between the core and outside-core survey areas in each of the two years of systematic surveys. All tests were two-tailed.

1.4 Results

Of the 7,864 nestlings banded prior to fledging during 1996-2008, 617 (7.8%) were recaptured in subsequent years. Approximately 78% of one-year-old recruits were recaptured on their natal patch of breeding habitat. The median natal dispersal distance of one-year-old banded recruits ($n = 390$) did not differ between the sexes (Table 1, U -test, $z = 1.03$, $P = 0.29$), therefore I pooled across sex to derive the distribution of natal dispersal distances (Fig. 2). The overall median dispersal distance was 1.42 km and the distribution of all natal dispersal distances was skewed and leptokurtic (skewness = 2.73; kurtosis = 9.54).

Systematic survey for banded recruits

There was no significant difference in the proportion of suitable habitat surveyed within the core and outside-core study areas (Table 2, $\chi^2 = 0.33$, $P = 0.56$). During the systematic surveys in 2008 and 2009, I examined 1327 and 1401 breeding adults, respectively (Table 3). The proportions of banded recruits observed within the core did not differ between the sexes in either year (χ^2 , $P > 0.10$), therefore the observations of males and females were pooled for further comparisons. The proportion of banded recruits observed among the surveyed breeding adults was significantly greater within the core survey area than the outside-core area during 2008 and 2009 (Table 3, χ^2 , $P < 0.01$). Only two banded recruits were detected in the outside-core survey area; both individuals were observed separately ~ 5.25 km from the nearest nest box study site. There was no significant year effect on the proportion of observed banded recruits in either survey area (χ^2 tests, $P > 0.10$).

1.5 Discussion

In contrast with the current assumption that juvenile Neotropical migrants tend to disperse to distant and unknown breeding locations, the results of this study indicate that juveniles tend to return

close to their natal location to breed. Based on banding data from 390 first-year recruits captured during 1997-2009, a predominant pattern of short-distance natal dispersal was apparent. Approximately 78% of observed banded recruits returned to breed within 3 km of their natal location and the median natal dispersal distance was 1.4 km. Likewise, the overall distribution of natal dispersal distances was extremely skewed and leptokurtic. With multiple dispersal options (over 20 nest box sites) positioned across an 18-km-wide nest box system, it was surprising that the observed natal dispersal distances were as short as they were.

The result of the systematic surveys outside the nest box study area provided support for the legitimacy of the distribution of natal dispersal distances calculated from the long-term nest box study. The chance of finding banded recruits is likely greater within the nest box study sites than outside, therefore the proportions of recruits observed may not reflect the actual proportions existing off of the nest box sites (Ronce 2007). I found, however, that the birds surveyed in the core area had a higher proportion of local recruits than the outside-core area and both areas were without nest boxes and had similar detection probabilities. Among all of the adults surveyed within the outside-core survey area (2008, n = 850; 2009, n = 963), I only detected two banded recruits. Each banded recruit was located just over 5 km from the nearest nest box site. In contrast, I found 46 banded recruits in the core survey area in 2008 and 31 in 2009. Estimates of juvenile recruitment are affected by the proportions of adults surveyed, and one should be cautious in interpreting the dispersal patterns based on comparing proportions alone (Cunningham 1986). However, I sampled an equal proportion of suitable habitat between the two survey areas and only detected two banded recruits within the outside-core survey area. Based on the proportions of recruits observed and the dispersal distribution, I concluded that individuals rarely (< 5% of the time) move beyond 8 km.

The configuration of nest box study sites within the core area could potentially affect the natal dispersal distances of prothonotary warblers. Since the juveniles banded in this study all fledged from nest boxes, juveniles returning to the region to breed may search for nest boxes rather than suitable habitat. This potential behavior could dramatically reduce the overall dispersal pattern. However, there was no significant difference in the natal dispersal distance of individuals that switched from their natal site to a new nest box site (median = 1940 m) versus those that returned to breed in the interstitial suitable breeding habitat where there were no nest boxes (median = 2160 m) (*U*-test, *P* = 0.14). If juveniles were returning from winter grounds and simply searching for nest boxes within the region, then the shape of the overall natal dispersal distribution would likely be more uniform.

Overall, female-biased natal dispersal is the predominant pattern reported in birds; however, male-biased natal dispersal and similar dispersal distances between the sexes have also been reported (Clarke et al. 1997; Greenwood 1980). Sex-biased dispersal can even differ between populations of the same species, potentially reflecting population-level variation of the sex-specific costs and benefits of dispersal (Balbontin et al. 2009). I found no evidence of sex-biased natal dispersal in this population and there was no significant difference in the proportions of banded recruits observed between males and females. My systematic survey for banded recruits was not, therefore, biased due to differences between the sexes in the propensity to disperse.

I found no significant variation in the probability of detecting banded recruits between the core and outside-core survey areas. Some banded recruits were likely missed during this survey, but there was no indication my playback surveys were significantly biased between the two survey areas. Furthermore, the relatively high estimate of detection probability of banded recruits (0.89) indicates 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.

Previous studies using mark-recapture techniques to document the natal dispersal of migratory species often have had difficulties differentiating between the effects of sampling bias and actual short-distance dispersal distributions. This inherent sampling bias is dependent on the size of the study area in relation to the actual dispersal distances of the study organism (Koenig et al. 1996). Individual movements greater than the diameter of the study area will not be detected, whereas, nearly all philopatric individuals are relocated (Koenig et al. 1996). Although the large-scale banding effort effectively reduced some of the inherent sampling bias, I further corrected for this bias by expanding the survey area. For two years, I systematically surveyed a majority (~78%) of suitable habitat within a 30 km buffer in all directions surrounding the source banding sites. Combining the diameter of the nest box study area (18 km) and expanded survey areas, natal dispersal movements up to 48 km could have been detected. Previous reports of maximum natal dispersal distance, re-scaled in units of median dispersal distances to compare between species of different mass, were typically < 23 median dispersal units (Sutherland et al. 2000). My systematic survey expanded search efforts to include long-distance movements of approximately 21 to 34 times the estimated median natal dispersal distance for prothonotary warblers. Individual natal dispersal movements of > 30 km are certainly possible for this population, however these long-distance movements are likely rare.

The prevailing pattern of short-distance dispersal that I found may be representative of other populations of migratory passerines. For example, Winkler et al. 2005 summarized data from one of the largest study areas and sample sizes for a Neotropical migrant to date and found that most juvenile tree swallows (*Tachycineta bicolor*) returned to breed within 10 km of their natal location while long-distance dispersal occurred very infrequently. This study reported a median natal dispersal distance of only 2.8 km for the tree swallows, but the researchers were limited in their ability to sample a majority of the habitat available in their vast study area. Similar patterns of short-distance dispersal have been documented in migratory songbirds from various families including indigo buntings (*Passerina cyanea*)

(Payne 1991), willow flycatchers (*Empidonax traillii*) (Sedgwick 2004), great reed warblers (*Acrocephalus arundinaceus*) (Hansson et al. 2002), and ortolan buntings (*Emberiza hortulana*) (Dale 2010). However, until study areas are expanded, it will be difficult to determine if short-distance natal dispersal in migratory songbirds is more prevalent than previously thought.

The apparent low natal philopatry (i.e. < 10%) documented in previous studies of migratory passerines may be attributable to relatively low juvenile survival, and not necessarily the result of a dominant pattern of long-distance natal dispersal. While juveniles may return to their natal site at rates lower than expected, juveniles may have returned to adjacent suitable habitat nearby (Lambrechts et al. 1999). While I agree that many estimates of natal dispersal from previous studies were biased, expanded study areas or the use of area-corrected statistical methods could be used when attempting to investigate juvenile survival (Cooper et al. 2008). Lacking actual estimates, juvenile survival is often assumed to be approximately 0.30 or one half of what adult survival is thought to be, and these values have been used to determine how much reproduction is needed to have stable populations (Faaborg et al. 2010b). However, due to limited study areas and reduced detection probabilities, previous estimates of adult survival are likely underestimated. In an experimental manipulation of breeding success, 80% of the previously successful adults returned in the following year (Hoover 2003). If adult survival is closer to 0.80, population stability could be achieved with little change in reproductive output even with juvenile survival rates that are far less than one-half of adult survival. Without accurate information on both breeding and particularly natal dispersal, previous studies may have over-estimated adult survival while under-estimating juvenile survival.

The fitness-related costs of natal dispersal, whether to fecundity or survival (Johnson and Gaines 1990; Pasinelli et al. 2004), could explain the pattern of short-distance dispersal observed in this population. Individuals may incur a greater probability of mortality caused by increased predation or

starvation with increased distance from the natal site. However, compared to the costs associated with migrating thousands of kilometers prior to returning to the region (Silllett and Holmes 2002), the influence of mortality for individuals dispersing between natal and subsequent breeding sites is likely minimal. Alternatively, if knowledge gathered prior to migration in the previous year increases the success of subsequent breeding attempts, then a pattern of short-distance dispersal would be favored (Bensch et al. 1998). The chances of inbreeding may increase as natal dispersal decreases (Hansson et al. 2007) (but see Wheelwright and Mauck 1998), potentially resulting in deleterious genetic combinations and subsequent fitness costs. Individuals do not, however, appear to actively avoid their natal area and, on two occasions, were found breeding in their natal nest box (but not with their parents or siblings). This result supports the dispersal-cost hypothesis proposed by Weatherhead and Forbes 1994, in which migratory individuals return near their respective natal area, but neither seek out or actively avoid the natal site.

Moving forward, studies of natal dispersal in migratory songbirds should expand study areas in an attempt to more accurately measure dispersal distances. With an increasing number of migratory species breeding within fragmented landscapes, studies should focus on the potential effects of habitat fragmentation on natal dispersal and, ultimately, juvenile survival. Distinguishing between dispersal and mortality is extremely vital to management and conservation issues. Population models relying heavily on the current estimates of juvenile survival are likely inaccurate and better information is needed. Similarly, management and conservation require the best available data for population models and estimates of dispersal parameters in order to assess the vulnerability of various species to changes in land-use and climate (Faaborg et al. 2010a). If natal dispersal distances in migratory songbirds are in fact much shorter than once thought, then local conservation efforts that improve the nesting success for migratory songbirds may directly benefit local populations by increasing local recruitment.

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1.7 Tables and Figures

Table 1. Descriptive statistics for natal dispersal of one-year-old prothonotary warblers in southern Illinois that fledged during 1996-2008.

Sex	Median (km)	Mean (km)	SE	Range	n
Male	1.45	2.28	1.87	0.03-16.17	192
Female	1.41	2.06	1.68	0.01-17.00	198

Table 2. Proportion of suitable habitat surveyed in expanded survey area in 2008 and 2009. Core represents the survey area located interstitially between nest box sites and up to 5 km surrounding nest box study area. Outside-core represents habitat from 5 km up to 30 km surrounding nest box study area.

Survey area	Suitable habitat (km ²)	Proportion of habitat surveyed
Core	9.65	0.846
Outside-core	25.05	0.757

Table 3. Proportions of the surveyed breeding adult population in expanded survey area that were banded recruits. Core represents the survey area located interstitially between nest box sites and up to 5 km surrounding the nest box study area. Outside-core represents habitat from 5 km up to 30 km surrounding the nest box study area.

Survey area	2008		2009	
	Proportion of banded recruits	Total adults observed (n)	Proportion of banded recruits	Total adults observed (n)
Core	0.096	477	0.071	438
Outside-core	0.002	850	0.000	963

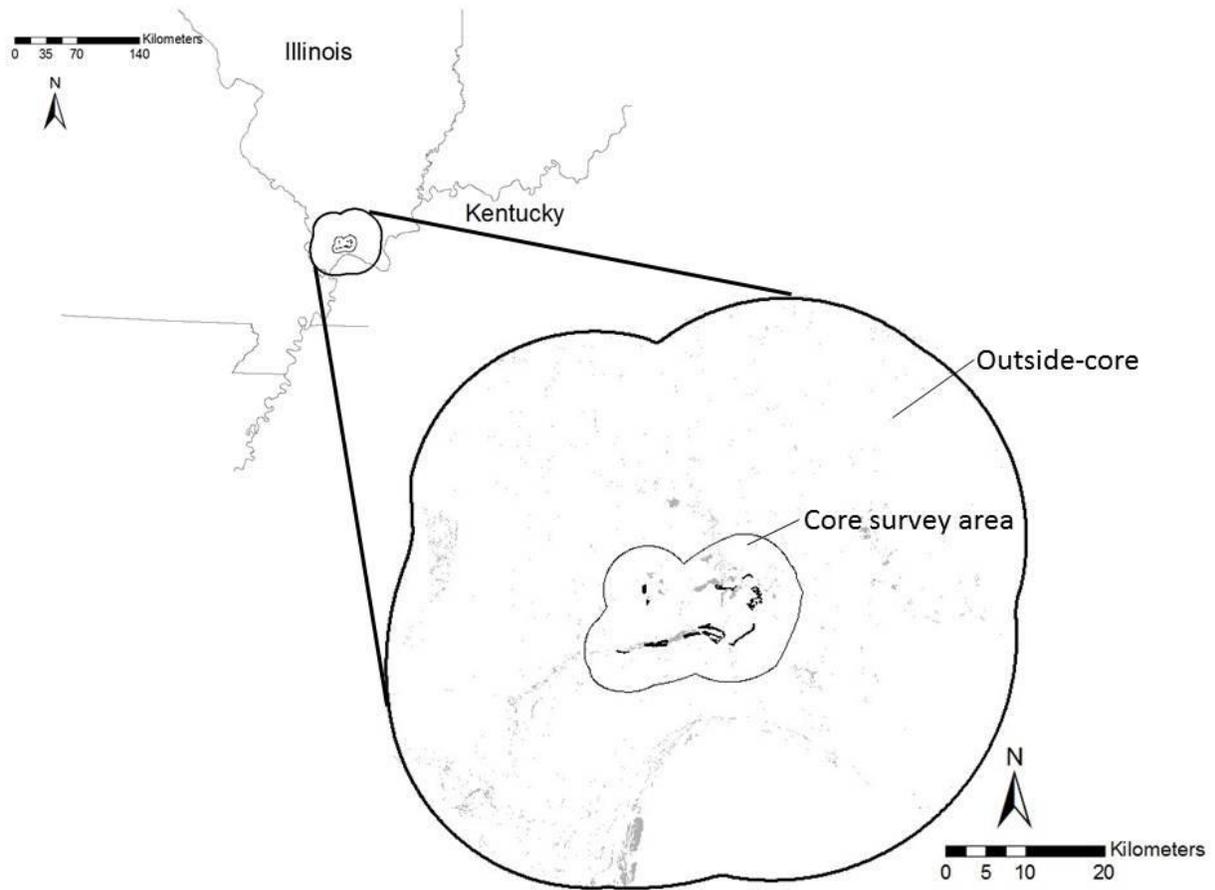


Fig 1. The entire study area in Illinois and Kentucky, depicting suitable habitat (light gray) determined by land cover data (Illinois State Geological Survey; Kentucky Geography Network). Black patches within core survey area indicate nest box study sites located in Cache river watershed.

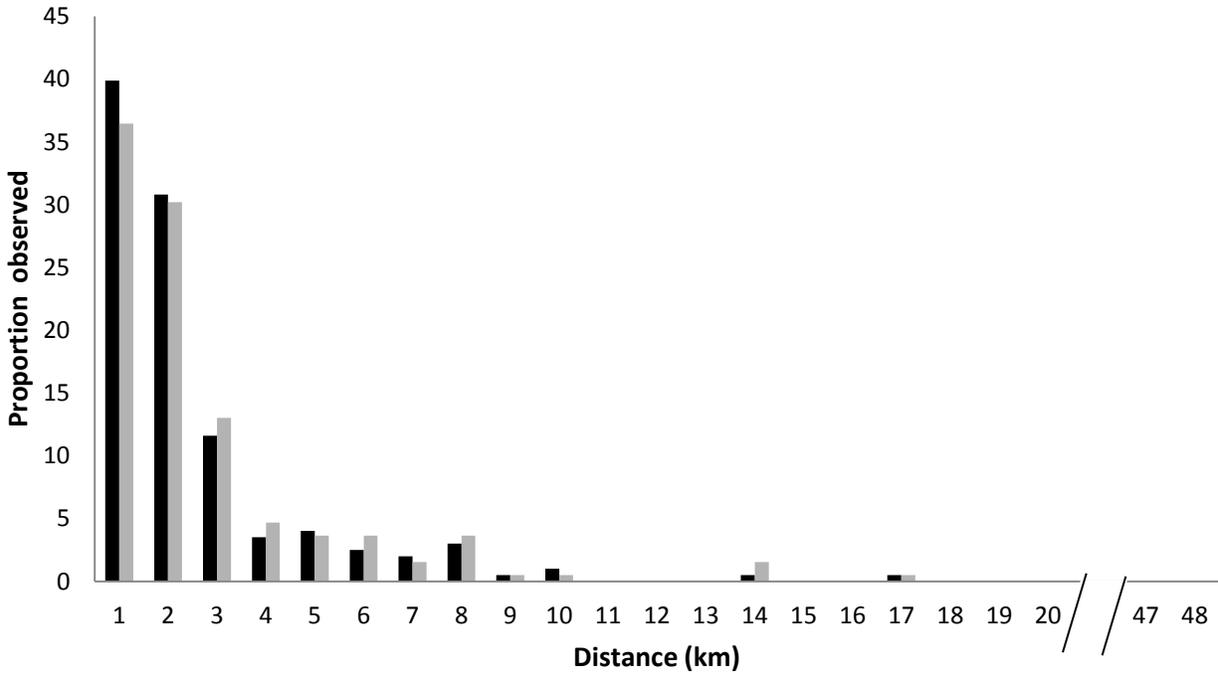


Fig. 2 Distribution of natal dispersal distances for 198 female (black) and 192 male (gray) one-year-old prothonotary warblers in southern Illinois, 1997-2009. Individuals were recaptured on nest box study sites and within the systematic survey area. Because there were no observations documented between 17 km and 48 km, the data was plotted on a broken x-axis

CHAPTER 2

Season and brood parasitism both affect first-year survival in a Neotropical migratory songbird

2.1 Summary

1. Juvenile survival is one of the most influential demographic parameters within vertebrates. Because first-year (i.e. 1-year-old) migratory passerines are thought to return to breed at great distances from their natal location, the factors that impact variability in survival between fledging and the first breeding attempt (i.e. first-year survival) have not been thoroughly investigated in migratory songbirds.
2. Using multi-state mark-recapture methods, I investigated the factors that affect first-year survival in prothonotary warblers (*Protonotaria citrea*) within a nest box study system in which we had previously documented patterns of short-distance natal dispersal. Incorporating natal dispersal distance into a multi-state model framework, I accounted for the potential confounding effect of dispersal distance on recapture probabilities for 6,093 warbler nestlings that fledged during 2004 through 2009. I examined the effects of season (fledging date), presence of a cowbird nestmate, brood size (number of warbler nestlings in the brood), and nestling body condition on first-year survival probabilities.
3. On average, first-year survival rates were nearly twice as high for individuals reared without cowbird nestmates (noBHCO = 11%) than those that were reared with a cowbird (BHCO = 6%). First-year survival rates decreased as the fledging date increased for noBHCO (ranging from 24% to 4%) and also decreased, although less sharply, for BHCO (ranging from 10% to 4%).
4. There was no significant effect of these explanatory factors on detection or transition probabilities, suggesting that the effects of fledging date and cowbird nestmates on survival were not produced by any confounding effects of these two factors on recapture probabilities.

5. By accounting for the potential confounds of recapture probabilities in a population with documented patterns of short-distance natal dispersal, this study presents one of the most robust estimates of first-year survival in a migratory songbird to date.

Key-words: costs of cowbird parasitism, capture-mark-recapture, local recruitment, natal dispersal, post-fledging survival, timing of breeding

2.2 Introduction

Most birds are capable of breeding when they are one year old. For birds, survival between fledging and the first reproductive attempt (first-year survival) is one of the most influential demographic parameters contributing to population growth (Robinson *et al.* 2004; Sim *et al.* 2011). Reliable estimates of first-year survival rates for migratory passerines are exceedingly rare at best (Faaborg *et al.* 2010). In lieu of reliable estimates of first-year survival, population modelers have used arbitrary values thought to represent adequate population-level replacement rates, such as one-half of adult survival (Faaborg *et al.* 2010). These arbitrary estimates are based on scant data, and even less is known regarding the effects of various breeding season phenomena on first-year survival rates. Identifying factors that influence first-year survival is necessary to increase the accuracy of these estimates and, ultimately, elucidate the causes of population growth or decline.

The timing of reproduction is considered one of the most significant decisions affecting reproductive success in birds, and individuals are typically able to successfully fledge more offspring earlier in the breeding season (Perrins 1970; Verhulst & Nilsson 2008). In non-migratory avian populations, post-fledging survival and local recruitment (i.e. the probability of a juvenile breeding within the study population in a subsequent year) decreases with later fledging dates and reduced body condition (Naef-Daenzer, Widmer & Nuber 2001; Monros, Belda & Barba 2002; Verhulst & Nilsson

2008). Because long-distance migratory birds must choose when and where to breed upon arrival to breeding areas, while also leaving enough time for juveniles and adults to adequately prepare for migration to wintering grounds, the effects of season (i.e. fledging date) on first-year survival may be particularly important. Seasonal ecological factors (e.g. decreased food availability or increased risk of predation over the course of the breeding season) may further reinforce the importance of breeding early, as the survival of fledglings prior to migration has been found to decline throughout the breeding season (Adams, Skagen & Savidge 2006; Gruebler & Naef-Daenzer 2008). However, it remains unclear how the seasonal timing of fledging influences juvenile survival throughout the entire migratory cycle to the first breeding attempt.

In North America, the brown-headed cowbird, (*Molothrus ater* Boddaert), a generalist obligate brood parasite, is known to reduce reproductive success for numerous host species by reducing clutch size, hatching success, and nestling survival (Payne & Payne 1998; Hoover 2003c). For those avian host species that are smaller than cowbirds (< 30 g) yet capable of raising both cowbird and host offspring, fledging success is typically dramatically reduced (Rasmussen & Sealy 2006). Furthermore, fledglings reared with a cowbird nestmate exhibit a reduced probability of local recruitment (Payne & Payne 1998; Hoover & Reetz 2006), likely indicating an effect of brood parasitism on first-year survival. Consequently, if the effects of season and brood parasitism both affect first-year survival, the effect of being reared with a brood parasite may be particularly pronounced late in the breeding season when food resources are thought to be reduced (Siikamaki 1998).

Central to the factors limiting the estimation of first-year survival in migratory populations is the inability to accurately determine the dispersal propensity of juveniles between fledging and their subsequent first breeding attempt (Cooper, Daniels & Walters 2008). Natal dispersal, the movement between birth and first-breeding locations, has been assumed to be too vast in migratory passerines to

allow for the estimation of first-year survival (Faaborg *et al.* 2010). Furthermore, in most study systems, detection probability decreases with increasing dispersal distances from the natal location (Koenig, VanVuren & Hooge 1996), limiting one's ability to differentiate between mortality and dispersal. In most mark-recapture studies of migratory passerines, less than 5% of individuals marked prior to fledging are relocated in a subsequent year (Weatherhead & Forbes 1994). The extent of how the various confounding methodological limitations (e.g. number of nestlings banded, study area, study duration) interact with actual dispersal and mortality is unknown.

Incorporating the effects of dispersal into study design and statistical methodology are necessary to increase the accuracy of juvenile survival estimates (Anders & Marshall 2005; Cooper, Daniels & Walters 2008). Likewise, the potential factors that impact first-year survival should be integrated for more accurate estimates of survival in migratory populations. In studies where the probability of detection is < 1 , capture-mark-recapture models are often used to incorporate detection or recapture probabilities into estimates of survival. An extension of the Cormack-Jolly-Seber model, multi-state modeling procedures estimate the state-specific (e.g. location, reproductive status, behavior, etc.) probability of survival, recapture, and the probability of switching between states (transition probability) (Lebreton *et al.* 2009). Because the detectability of an individual may vary as a function of numerous factors (e.g. time, age, gender, location, etc.) multi-state modeling is a useful tool to account for potential biases generated by state-dependent recapture probabilities (e.g. reduced recapture probability of birds infected by *Plasmodium* (Jennelle *et al.* 2007)).

By defining natal dispersal distances as states in a multi-state framework, I assessed the importance of several factors that may affect first-year survival while simultaneously controlling for heterogeneity in recapture probabilities. Multi-state models typically include several parameters, thus making them inherently data hungry and in need of large sample sizes. The long-term study of

populations of prothonotary warblers (*Protonotaria citrea* Boddaert) breeding in southern Illinois provides an unprecedented opportunity to use multi-state mark-recapture models to estimate first-year survival rates in a Neotropical migratory songbird. I have previously documented patterns of short-distance natal dispersal in these warblers within this study system (see Chapter 1); therefore estimates of first-year survival from this study system should be relatively robust.

Using this novel multi-state approach, I first examined whether recapture probabilities were influenced by natal dispersal distances. I predicted that recapture probabilities for individuals dispersing farther (> 6 km from natal location) would be lower than for individuals with shorter natal dispersal distances. Next, while accounting for potential effects of natal dispersal distances on detection probabilities, I investigated the effects of season (fledging date), brood parasitism (reared with or without a cowbird nestmate), nestling body condition and brood size on first-year survival. In particular, I predicted that first-year survival probabilities would decrease with fledging date, the presence of a cowbird nestmate, and reduced nestling body condition. I included the number of warbler nestmates to account for a potential relationship between increased brood size and predation risk (Gotmark 2002). Finally, I determined whether the severity of the effects of brood parasitism on first-year survival varied seasonally and predicted that survival rates would be lowest for individuals reared later in the season in the presence of cowbird nestmates.

2.3 Materials and Methods

Species and study area

Data for this study were collected from 2004 to 2010 in the Cache River watershed (37°18'N, 88°58'W) in southern Illinois, USA. Populations of breeding prothonotary warblers were studied within wet forested habitat that included fragmented flooded bottomland forests, sloughs, and swamps (Hoover 2001). Prothonotary warblers are long-distance migratory passerines that winter in the Neotropics and breed throughout the eastern portion of the United States. These warblers are non-excavating cavity nesters that breed almost exclusively within forested wetlands, nesting near or over water (Petit 1999), and breed from late April to early August in the area where this research took place (Hoover 2003a). Prothonotary warblers will readily use nest boxes when available and are commonly parasitized by brown-headed cowbirds (Hoover 2003b; Hoover 2003c).

Field methods

Each year, nest boxes (approximately 1500) were placed among 20-25 study sites situated within an area 18 km in length by 12 km in width. Within sites, nest boxes were placed in a grid pattern (40-50 m spacing) within appropriate breeding habitat. Nest boxes were positioned 1.7 m above ground and had 44-mm-diameter openings, similar to the attributes of natural cavities used by adult warblers in this study system (Hoover 2001). Nest boxes were monitored every 3-6 days throughout each breeding season. At each active nest, the number of warbler and cowbird eggs and nestlings was recorded and the fate of the nest attempt (offspring fledged or not) determined. Nestlings were assumed to have fledged if they reached fledging age (10-11 days) and the nest was empty and intact. Additional evidence that nestlings had fledged included the presence of trampled droppings in the bottom of the nest, alarm calls from adults nearby, and direct observations of appropriately-aged fledglings in the relevant territory. Nestlings that did not survive to fledge (deceased individuals within a brood or whole brood lost to nest predation) were removed from the analyses. Each nestling was banded with a uniquely-numbered aluminum U.S. Geological Survey band on its right leg prior to fledging when they

were 5-8 days old. The mass (to the nearest 0.25 g) and tarsus length (to the nearest 0.5 mm) of each nestling was measured during the banding process.

I 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, I determined the origin of each banded recruit and determined their dispersal distance by measuring the straight-line distance between natal nest boxes and first recapture locations. 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 playback with a decoy placed next to a mist-net and female recruits were captured while incubating by placing a small plastic bag over the nest box opening. All banded recruits and other breeding adults were marked with a unique color-combination. I assigned adults to each active nest based on territorial boundaries and the presence of males and females at individual nest boxes and knew the identity of > 95% of the adults on each nest box study site each year.

Modeling framework

Concerned that recapture probability may be affected by natal dispersal distance, I used multi-state mark-recapture in program MARK (White & Burnham 1999) to incorporate the transition of an individual from fledging to one of four distance categories (< 2 km, 2-4 km, 4-6 km, and > 6 km) in a subsequent breeding season into the analyses. In contrast to single-state Cormack-Jolly-Seber (CJS) modeling, multi-state mark-recapture allows for the simultaneous age- and state-specific estimation of apparent survival (ϕ), recapture probability (p), and transition probabilities (Ψ) between states; in this case distance categories. In each individual encounter history, observations were classified as one of six states: state 1 was the initial marking as a juvenile prior to fledgling; states 2-5 included local recruitment into one of four dispersal distance categories; and state 6 was an 'absorbing state'

representing the individuals captured in breeding seasons after initial capture occasion. For example, an encounter history of 0126600 indicates the chick was initially marked in 2005, recaptured in state 2 (distance category < 2km) in 2006, and relocated again in state 6 ('absorbing' adult state) in 2007 and 2008. Because individuals in state 1 are not recaptured until dispersing to one of four distance categories in a subsequent breeding season, the detection probability of state 1 was fixed to zero. Transitions between state 1 directly to state 6 and transitions among distance categories (states 2-5) were not possible in this framework and were constrained to zero. To estimate recapture, transition and survival probabilities during the first-year, two age classes were used: first-year and pooled after-first-year (adult).

Model selection and goodness-of-fit

To assess the goodness-of-fit (GOF) of the data, I used program U-Care (Choquet *et al.* 2009) to compare the fit of the data with the JollyMoVe (JMV) model, which allows encounter probabilities to vary by the previous state. Model selection was based on QAIC_c (Akaike's Information Criterion modified by the variance inflation factor, \hat{c} ,) and QAIC_c weights (Burnham & Anderson 2002). Model-averaging was used to report parameter estimates. To minimize the number of potential models, I used a three-step approach to determine the most parsimonious model structure for transition probability, recapture probability and apparent survival. First, I modeled transition probability while apparent survival varied among age-classes, and recapture probability varied between the two age-classes and among states. Using the top-ranked transition probability structure, I modeled a set of recapture probabilities while continuing to use an age-dependent survival structure. In the final step, the best transition and recapture probability structures were then applied to survival models.

Model covariates

To investigate the influence of four explanatory variables on apparent survival, the number of warbler nestlings reared within the brood, presence of a cowbird nestmate, fledging date, and body condition were included in the *a priori* survival model set. Warblers reared with a cowbird nestmate (BHCO) and without (noBHCO) were classified into separate groups to determine if fledging date affected warblers with a cowbird nestmate more severely. Residuals from an ordinary least squares (OLS) linear regression of body mass on tarsus length were used as an index of nestling body condition (Schulte-Hostedde *et al.* 2005). I projected the fledging date of each individual by estimating the nestling age during banding and assumed fledging at 10 days old (Petit 1999). I was unable to determine the sex of nestlings at the time of banding and thus excluded sex from the apparent survival analysis.

Explanatory variables were considered statistically significant if their 95% CI (adjusted for \hat{c} value) excluded zero. Correlations among model covariates were examined to ensure that highly correlated variables ($|r| > 0.70$) were not included within the same model. Model covariates from the top-ranked survival models were interchanged with the recapture structure to ensure covariate effects were not generated by variation in detectability. Data analysis other than multi-state mark-recapture was performed using SAS (version 9.2) and parameter estimates with ± 1 standard error are given.

2.4 Results

I analyzed the encounter histories of 6093 individuals banded as nestlings, of which, 418 individuals were recaptured in a subsequent year. Although I was unable to determine sex prior to fledging, a similar number of males ($n = 212$) and females ($n = 206$) were recaptured, suggesting that differences in first-year survival or recapture probabilities between the sexes may be small. The test for GOF indicated some lack of fit between the data and the JMV model (sum; $\chi^2 = 23.44$, d.f. = 14, $P = 0.05$). To reduce potential effects of overdispersion and bias, I incorporated an estimated variance inflation factor ($\hat{c} = 1.67$) based on the sum of the GOF tests (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 ($\Delta\text{QAIC}_c = 120.37$). There was little support for annual variation in transition probabilities (increase $\text{QAIC}_c = 5.61$). The transition model with the greatest support ($\Delta\text{QAIC}_c = 4.82$ over next best model) 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. Transition probabilities decreased dramatically with distance (Fig. 3), with the highest probability of local recruitment within the < 2 km distance category (0.68 ± 0.02). This transition structure was used to model subsequent recapture and survival analyses.

Recapture probabilities

Contrary to expectations, recapture probabilities from this study did not decrease with increased dispersal distance. In a model that included variation in first-year recapture probabilities among distance categories ($p_{age,f}$), 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 there was no support for distance-related first-year recapture probabilities, models incorporating annual variation were better supported (Table 4). However, a model including annual variation in first-year recapture probabilities and variation among distance categories was not highly ranked ($\Delta\text{QAIC}_c = 18.30$). The top-ranked recapture model incorporated an effect of year on first-year recapture probabilities and constant probability for ages > 1 year old (Table 4; Fig. 4). Annual variation in recapture probability for first-year warblers varied between $0.56 (\pm 0.06)$ and $0.28 (\pm 0.05)$ whereas recapture probability for individuals after being recruited was greater (0.75 ± 0.03) (Fig. 4). This reflects high return rates of adults once they have bred on the study sites (Hoover 2003a).

Survival probabilities

Incorporating the top-ranked transition and recapture structures, models incorporating two age-classes in apparent survival estimates were better supported than when compared to a constant model ($\Delta\text{QAIC}_c = 39.88$). Annual variation in first-year apparent survival was not supported when compared to the age-class model (Table 5). Thus, individual covariates were applied to a two age-class model that included time-constant apparent survival estimates.

First-year apparent survival varied as a function of fledging date and with presence of a cowbird nestmate (Table 5; Fig. 5). The top ranked model (Model 8; Table 5), included similar linear trends for the effect of fledging date on individuals reared with a cowbird nestmate (BHCO) and without (noBHCO). Overall, all models $< 10 \Delta\text{QAIC}_c$ included fledging date, and model averaged estimates of first-year apparent survival declined throughout the season both for individuals reared with and without a cowbird nestmate (Fig. 5). Similarly, while holding other covariates at mean observed values, model averaged apparent 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) (Fig. 6). There was some support for an interaction between the effects of fledging date and cowbird parasitism on first-year survival. The model fit was slightly improved by removing the effect of date for group BHCO (Table 5; 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) (Fig. 5).

There was marginal support for nestling body condition (*cond*) to predict first-year survival. Despite a model incorporating condition having nearly equal support to the top-ranked model (Model 9; $\Delta\text{QAIC}_c = 0.47$), 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 apparent

survival covariate structures were interchanged with the recapture probabilities, QAIC_c decreased by > 2, suggesting that variation in apparent survival was not being driven by the effects of explanatory variables on recapture probabilities.

2.5 Discussion

Seasonal decreases in the probability of local recruitment have been reported in resident populations (Verhulst & Nilsson 2008), but my study is the first to document a seasonal decrease in first-year survival in a migratory bird species. Throughout the breeding season, first-year survival estimates for non-parasitized warblers decreased from 0.22 (\pm 0.02) to 0.03 (\pm 0.03), with a substantial reduction during the first month (Δ 0.12). Parental quality and seasonal ecological factors, the two main non-exclusive hypotheses explaining seasonal variation in reproductive performance (Verhulst & Nilsson 2008), could also explain this decrease in the probability of first-year survival across the breeding season. 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 (Moller, De Lope & Saino 2004). However, the parental quality hypothesis alone fails to explain the dramatic seasonal decrease in first-year survival. From 2004-2009, a majority (> 65%) of the adult females fledging offspring late in the season had 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 than they are because most 'high quality' individuals (i.e. early breeding birds) breed a second time. Likewise, studies that manipulated reproductive timing by cross-fostering young found support for both the timing and quality hypotheses (Verhulst & Nilsson 2008).

The ability to breed early may reduce the effects of seasonally varying ecological factors on first-year survival. Previous studies have documented the importance of food availability (Adams, Skagen &

Savidge 2006), predation (Gotmark 2002), nest ectoparasites (Streby, Peterson & Kapfer 2009) and immunity (Cichon & Dubiec 2005) on post-fledging survival in passerines. Throughout the breeding season, the influence or intensity of these factors may increase, thus reducing survival of fledglings prior to migration. Lacking the ability to use previous migratory movements for navigation, juveniles may incur a greater risk of mortality during fall migration than adults (Reilly & Reilly 2009), thereby reducing first-year survival. 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.

Of the nestling warblers that fledged, the probability of first-year apparent survival was approximately 40% lower for those reared with a parasitic cowbird nestmate than for those reared with only host nestmates. During the nestling stage, cowbirds are typically able to out-compete their host nestmates for food (Lichtenstein & Sealy 1998; Kilner, Madden & Hauber 2004) and nestling body mass is often found to be reduced in parasitized nests (Hoover 2003c). Surprisingly, I found no significant difference (ANOVA; $F_{1,6085}$, $P = 0.83$) in body condition prior to fledging between individuals reared with or without a cowbird nestmate. It is possible that the impact of host-parasite competition on first-year survival occurs instead during the post-fledging stage, particularly if cowbirds continue to out-compete host fledglings for food once out of the nest (Woodward 1983; Rasmussen & Sealy 2006).

The risk of predation for fledglings is greatest during the first few days after leaving the nest (Anders, Faaborg & Thompson 1998). Competition between host and parasitic fledglings for food from the attending parents 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 (Gotmark 2002). In addition, cowbirds are one of the loudest-begging fledgling passerines (Woodward 1983) and any host fledglings in the vicinity of a loudly-begging cowbird fledgling may be more prone to predation (Hauber

& Ramsey 2003). Collectively, it may be difficult for host fledglings to avoid the increased predation risk associated with increased host and cowbird begging. Alternatively, the effects of cowbird nestmates on other potentially influential factors (e.g. immune function, nest ectoparasite load) not measured in this study, could account for the reduced probability of first-year survival for warblers raised with a cowbird.

The probability of first-year survival declined throughout the breeding season both for individuals reared with and without a cowbird nestmate. Contrary to my prediction, the negative effect of cowbird parasitism (i.e. the distance between the two trend lines in Fig. 5) on first-year survival rates of warblers was reduced as the breeding season progressed, so much so that survival rates of warblers reared with and without a cowbird nestmate were similarly low late in the season. This convergence of rates to a low point late in the season may reflect the importance of fledglings having as much time as possible to acquire adequate resources prior to migration. For birds fledging late in the breeding season, the cost of being reared with a cowbird may be overshadowed by a general lack of food resources, inadequate time available to prepare for fall migration, heightened predation on fledglings regardless of parasitism status, or all of the above. Alternatively, if post-fledging survival also decreases seasonally for *cowbirds*, the reduced effect of cowbird parasitism on first-year survival of warblers produced late in the season may be a result of reduced probability of late-season cowbird fledglings surviving, thereby removing cowbird competition with warbler fledglings for resources. Regardless of how these factors play out across the breeding season, it remains to be determined whether most of the first-year mortality occurs during the post-fledging period prior to fall migration, or whether the influence of the breeding season carries over to affect first-year mortality more during migration and over winter.

The relationship of season and brood parasitism may provide insights into cowbird-host co-evolution. For small birds unable to remove cowbird eggs, the development of a rejection strategy would likely involve nest desertion and re-nesting (Davies 2000), which would result in later nesting

dates. Because the impact of cowbird parasitism on first-year survival is diminished throughout the season, the formation of a rejection strategy may be advantageous to reproductive success. Likewise, as the probability of brood parasitism is often greatest at the beginning of the breeding season (Hoover, Yasukawa & Hauber 2006; Benson *et al.* 2010) the benefits of breeding early may be reduced. Therefore, the evolution of host rejection strategies could depend on the cost of parasitism, the probability of being parasitized during re-nesting attempts, and the cost of breeding later (i.e. rejecting the parasite and breeding again).

Few studies to date have been able to account for the potential effects of natal dispersal distances on detection probabilities and estimates of first-year survival, especially within an open population. The variables best explaining first-year survival rates in my study did not appear to affect natal dispersal distances and individuals reared without a cowbird or produced early in the season did not have a greater probability of returning close to home. When the individual covariates of the top-ranked models were incorporated into the recapture probability structures, the QAIC_c values decreased. Likewise, in a *post-hoc* analysis, the individual covariates failed to influence transition probabilities from the juvenile stage to discrete distance categories. Thus, my estimates of first-year survival were not confounded by nor an artifact of natal dispersal and the effects of fledging date and cowbird nestmates on survival rates are real.

The ability to differentiate between dispersal and mortality is of particular importance to studies using mark-recapture and vital to accurately estimate survival. Previous studies have documented a decline in the frequency of local recruits with increasing natal dispersal distances in migratory passerines (Payne 1991; Wheelwright & Mauck 1998; Winkler *et al.* 2005). However, with the exception of Winkler *et al.* 2005, study sites used to conduct research on migratory passerines are often small, resulting in biases towards documenting only short distance dispersal events (Koenig, VanVuren & Hooge 1996). In a

population exhibiting patterns of short-distance natal dispersal (see Chapter 1), I attempted to account for the potential effects of natal dispersal on recapture probability. Contrary to my prediction, the probability of detecting a natal dispersal event at the furthest distances observed (6-17 km), were similar to short-distance (< 2 km) movements. The limited variation in recapture probabilities in relation to natal dispersal distance reported in this study is likely a function of working within a relatively large study system (18 km x 12 km in size). Based on systematic surveys conducted in the majority of appropriate habitat within 30 km surrounding the nest box study system (see Chapter 1), long-distance dispersal and permanent emigration appear to be rare, suggesting that these are the most robust estimates of first-year survival for a migratory passerine to date.

Accurate estimates of first-year apparent survival in migratory passerines are lacking and population models incorporating demographic parameters have been limited to the use of arbitrary values, such as one half of adult survival (Ricklefs 1973), to represent first-year (i.e. juvenile) survival. A recent review by Faaborg *et al.* 2010 reported that published estimates of adult survival tend to center around 0.60 for a variety of migratory songbirds. This estimate for adult survival yields the arbitrary value of 0.30 for first-year survival, and these survival rates are then used to determine how much per capita reproductive output is needed to maintain a stable population. For prothonotary warblers, the maximum mean (i.e. without cowbird nestmates) first-year survival estimate of 0.11 is far less than 0.30. Additional support for relatively lower first-year survival rates has come from studies that have combined pre-migration and over-winter survival estimates (Holmes, Sherry & Reitsma 1989; Sillett & Holmes 2002) and obtained values between 0.18 and 0.24 (Adams, Skagen & Savidge 2006), between 0.15 and 0.18 (Reilly & Reilly 2009) and, in combination with estimates of site fidelity, 0.11 (Lehnen & Rodewald 2009). If true first-year survival is lower than previously thought, it would dramatically change (increase) the amount of reproduction needed for population stability or growth. If juvenile survival has been overestimated in migratory songbirds, it is possible that adult survival has been underestimated.

Experimental manipulations of reproductive success led to the discovery that adult survival in prothonotary warblers likely exceeds 0.80 (Hoover 2003a), indicating that low juvenile survival (i.e. 0.11) may be offset by very high adult survival. Whether these survival values are common or exceptional will become clearer as better estimates of survival emerge from other study systems.

As demonstrated in this study, the timing of reproduction is extremely influential to reproductive success and there is a large benefit to breeding early in the season. If global temperatures continue to increase and become more variable, climate change may dramatically affect the reproductive success of migratory passerines. In response to increasing spring temperatures, spring arrival and laying dates of many migratory populations are becoming earlier (Both & Visser 2001). The advanced arrival dates of migratory birds, however, may not perfectly match the observed temporal shifts in optimal food supply, leading to an 'ecological mismatch' and possible subsequent population declines (Both *et al.* 2006; Both *et al.* 2010; Jones & Cresswell 2010). At the same time, the effects of increasing temperatures may affect the probability of brood parasitism for some species (Saino *et al.* 2009; Moller *et al.* 2011) thereby reducing the benefits of nesting earlier in the breeding season.

My study demonstrates the importance of fledging date and brood parasitism to first-year survival estimates while taking into account detection probabilities and natal dispersal distances. Although there was no indication that natal dispersal distances influenced recapture probabilities in this study population, researchers attempting to improve the accuracy of first-year survival estimates should increase study area size and include surveys for recruits outside the study area when possible. It is now important to identify the mechanisms driving the seasonal pattern in first-year survival and focus on determining the relative importance of seasonal variation in food availability and predation on newly-fledged birds, the effects of cowbird nestmates on each of these factors, and whether the pattern is being driven more by first-year mortality occurring prior to versus after the start of fall migration.

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2.7 Tables and Figures

Table 4. Model selection to estimate capture probabilities for prothonotary warblers, *Protonotaria citrea*, in southern Illinois, USA, 2004-10.

ϕ	Ψ	p	QAIC _c	Δ QAIC _c	QAIC _c weight	No. par.	QDEV
ϕ_{age}	Ψ_f	$p_{age,time}$	4297.39	0	0.98	13	4271.34
ϕ_{age}	Ψ_f	p_{age}	4305.50	8.11	0.02	8	4289.48
ϕ_{age}	Ψ_f	$p_{age,f}$	4309.01	11.61	0.00	11	4286.97
ϕ_{age}	Ψ_f	$p_{age,time,f}$	4315.69	18.30	0.00	31	4253.39
ϕ_{age}	Ψ_f	p_{time}	4336.64	39.24	0.00	12	4312.59
ϕ_{age}	Ψ_f	$p_{.}$	4339.80	42.41	0.00	7	4325.79

ϕ , survival; Ψ , transition; p , recapture; QAIC_c, quasi-likelihood Akaike's information criterion corrected for small sample size; No. par., number of parameters; QDEV, $-2 \log\text{-likelihood}/\hat{c}$; *age*, age-class structure including first-year age-class and pooled age-class after first-year; *f*, state-dependent variation; *time*, annual variation; (.), indicates a constant for parameter.

Table 5. Model selection to estimate first-year apparent survival for prothonotary warblers, *Protonotaria citrea*, in southern Illinois, USA, 2004-2009.

No.	ϕ	QAIC _c	Δ QAIC _c	QAIC _c w _i	K	QDEV
Models without effect of cowbird parasitism on first-year apparent survival						
1	ϕ_{date}	4265.01	5.48	0.01	15	4234.94
2	$\phi_{date+cond}$	4265.44	5.91	0.01	16	4233.36
3	$\phi_{date+host\#}$	4266.34	6.81	0.00	16	4234.26
4	$\phi_{host\#}$	4296.37	36.84	0.00	15	4266.29
5	ϕ	4299.40	39.88	0.00	14	4271.34
6	ϕ_{cond}	4299.62	40.01	0.00	15	4269.55
7	ϕ_{time}	4303.56	44.04	0.00	19	4265.45
Modeling the effect of cowbird parasitism on first-year apparent survival						
8	$\phi_{(noBHCO = BHCO)+date}$	4259.53	0.00	0.23	16	4227.45
9	$\phi_{(noBHCO = BHCO)+date+cond}$	4259.99	0.47	0.18	17	4225.90
10	$\phi_{(noBHCO+date) \neq (BHCO)}$	4260.13	0.60	0.17	16	4227.43
11	$\phi_{[(noBHCO+date) \neq (BHCO)]+cond}$	4260.50	0.97	0.14	17	4226.41
12	$\phi_{(noBHCO+date) \neq (BHCO+date)}$	4261.30	1.78	0.09	17	4227.21
13	$\phi_{[(noBHCO+date) \neq (BHCO+date)]+cond}$	4261.74	2.22	0.07	18	4225.63
14	$\phi_{(noBHCO = BHCO)+date+cond+host\#}$	4261.92	2.39	0.07	18	4225.82
15	$\phi_{(noBHCO = BHCO)}$	4297.73	38.21	0.00	15	4267.66
16	$\phi_{(noBHCO = BHCO)+time}$	4306.83	47.30	0.00	24	4258.65

ϕ , apparent survival; QAIC_c, quasi-likelihood Akaike's information criterion corrected for small sample size; K, number of parameters; QDEV, -2 log-likelihood/ \hat{c} ; *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; \neq , indicates an interaction between terms; *time*, annual variation.

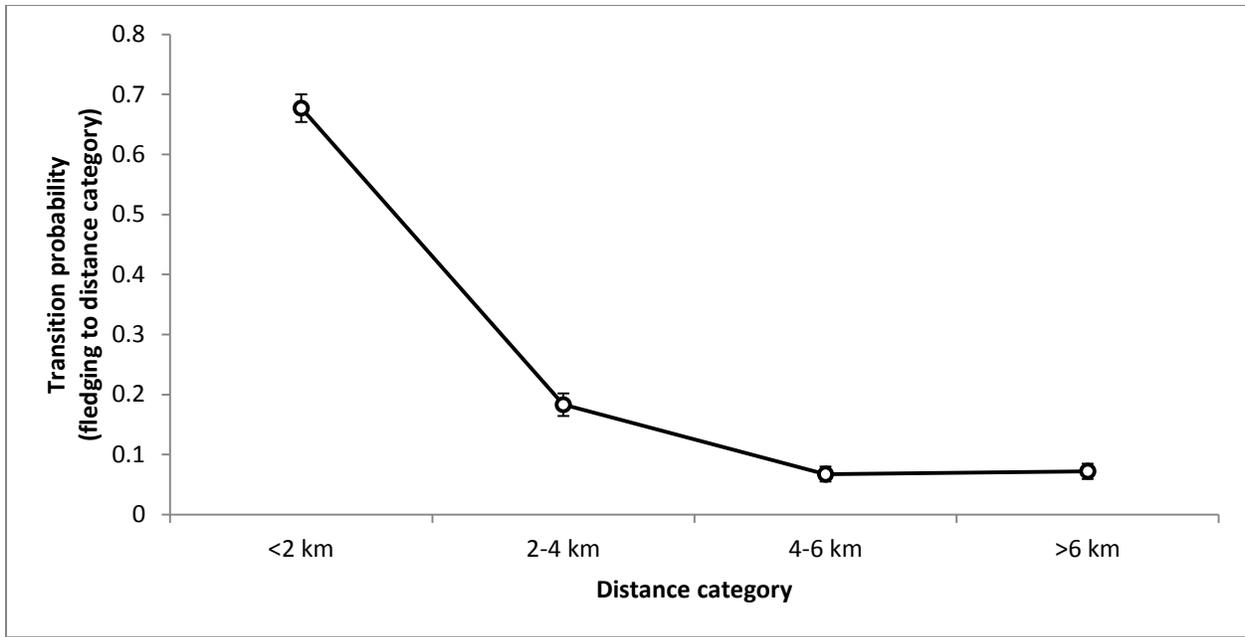


Fig 3. Probability (mean \pm 1SE) of transition between fledging and four distance categories for prothonotary warblers in southern Illinois, USA, 2004-2009.

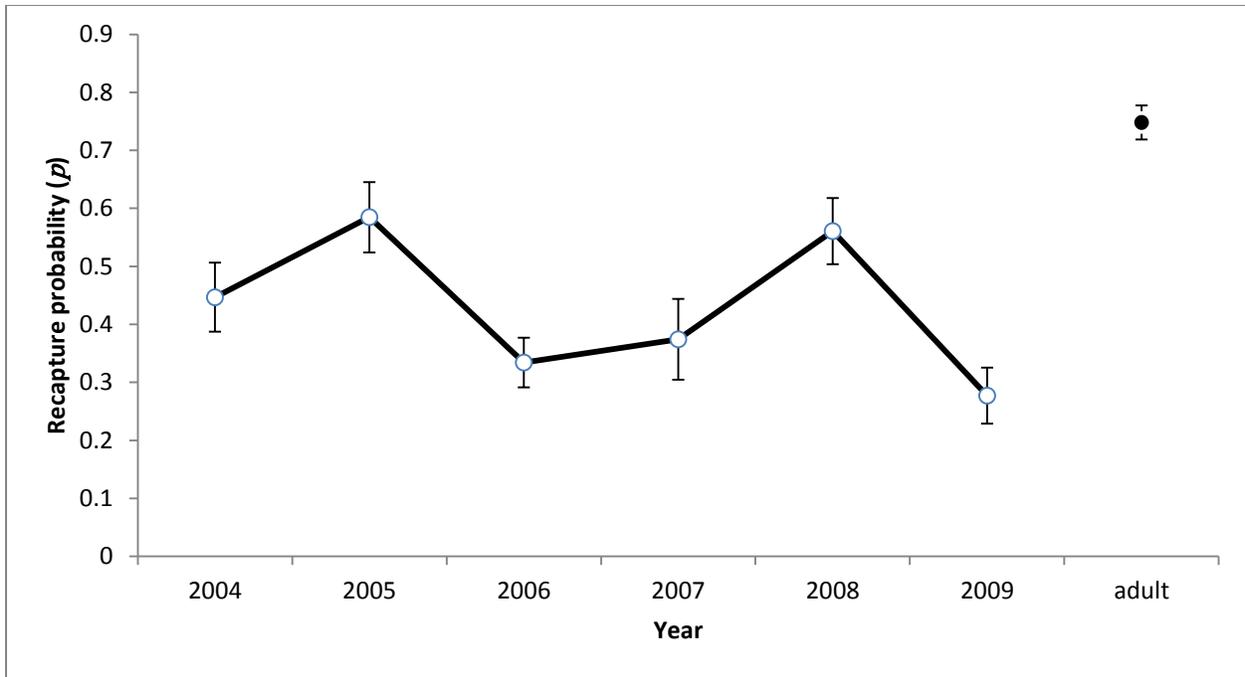


Fig. 4. Model averaged estimates of annual capture probabilities (mean \pm 1SE) for first-year (open circles) and > first-year (adult; closed circle) prothonotary warblers in southern Illinois, USA, 2004-2009. Adult recapture probability was modeled as constant across years.

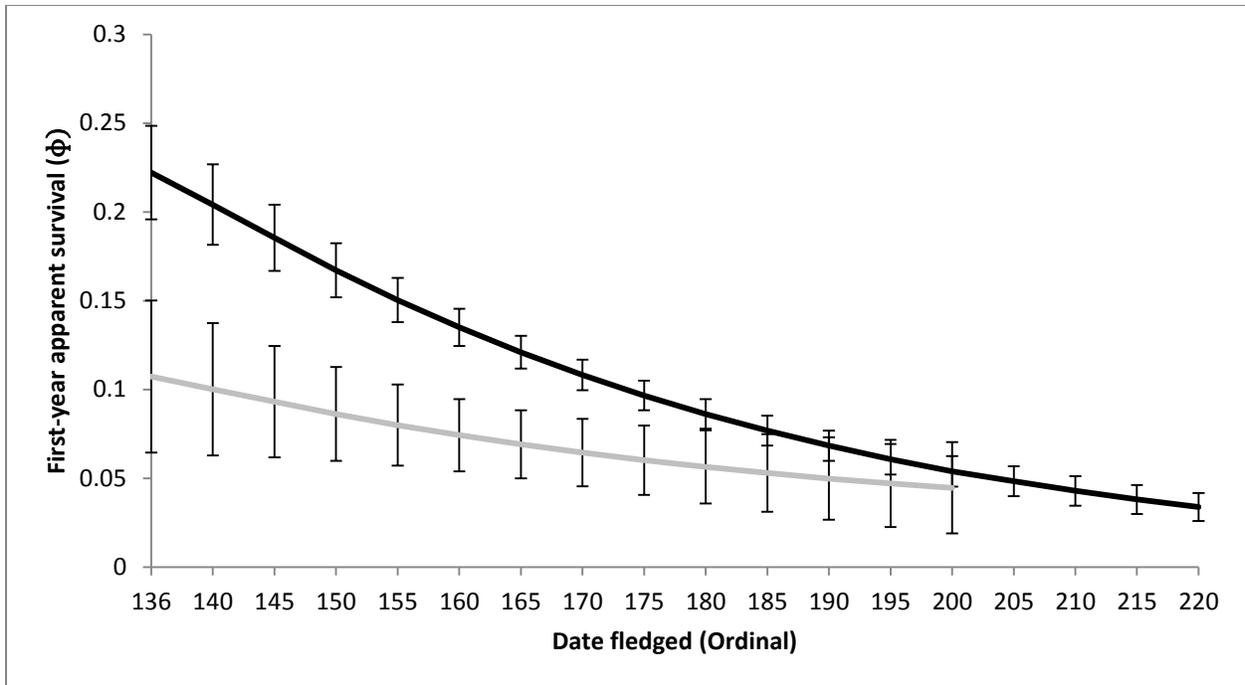


Fig. 5. Seasonal variation in model averaged estimates (mean \pm 1SE) of first-year apparent survival for prothonotary warblers reared with cowbirds (grey line) and in the absence of cowbirds (black line) in southern Illinois, USA, 2004-2009. All other variables were held at mean observed values.

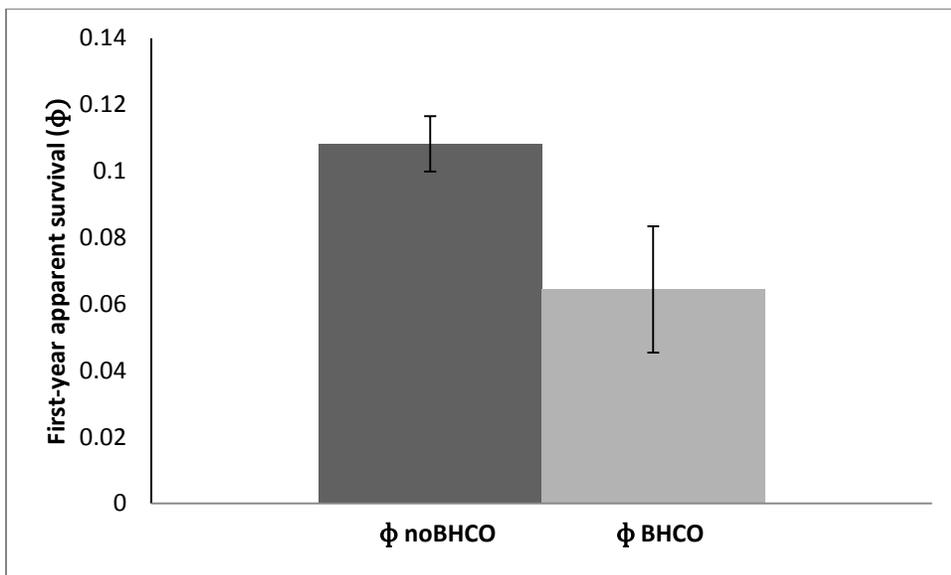


Fig. 6. Model averaged first-year apparent survival estimates (mean \pm 1SE) for prothonotary warblers reared without (noBHCO) and with (BHCO) a cowbird nestmate in southern Illinois, USA, 2004-2009. All other variables were held at mean observed values.

CHAPTER 3

Summary

Migratory songbirds produced in one area are thought to disperse to distant but unknown breeding habitats. The challenge of differentiating between long-distance natal dispersal and mortality in migratory birds has hindered our ability to adequately determine the predominant natal dispersal distances and accurately estimate first-year survival rates. The results from my study suggest that a vast majority of prothonotary warblers, a Neotropical migratory songbird, return to breed relatively close to their respective natal location. Using recent advancements in mark-recapture survival analyses, I accounted for the potential confounding effect of dispersal distance on recapture probabilities to investigate the factors that affect first-year survival. This is the first study to document a decrease in first-year survival with increasing fledging dates and for individuals raised with a cowbird nestmate in a migratory passerine. By documenting the pattern of natal dispersal, and thus differentiating between dispersal and mortality, the first-year survival rate is likely the most robust estimate to date. This estimate may help recalibrate juvenile survival estimates, which were likely overestimated in previous population models. With increasing global temperatures and habitat fragmentation, local and regional land managers can use the information from this study to direct conservation efforts.