

DOES WHAT YOUR NEIGHBORS DO MATTER? AN EXPERIMENTAL
EXAMINATION OF SEX DIFFERENCES IN THE USE OF PUBLIC AND PRIVATE
INFORMATION IN BREEDING DISPERSAL DECISIONS IN A MIGRATORY
SONGBIRD

By

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To Jeff, my best friend, my colleague and my partner

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For my doctoral research, I investigated sex differences in breeding dispersal decisions of a socially monogamous, territorial songbird, the prothonotary warbler (*Protonotaria citrea*). I used experiments to influence dispersal decisions based on public information, that is, conspecific reproductive success, and private information pertaining to the genetic mating system. Unsuccessful individuals are the most dispersive and therefore became the primary focus of my research. Males and females both appeared to use public information in their dispersal decisions. Males returned between years to good neighborhoods whereas females returned to good patches.

What appeared to be public information, in fact, was mostly private information. Unsuccessful male warblers based their between-year neighborhood fidelity on either the fledging of extra-pair (EP) offspring, or if unsuccessful on all fronts (i.e., own nest and EP mating), neighborhood quality. Unsuccessful females, in contrast, returned between years to their patch if they had cuckolded their mate, but moved farther based on the relatedness to their social mate. Females were more likely to cuckold their social mate the more closely they were related.

Further experimental examination of male dispersal decisions revealed that males were aware of their fledged EP offspring. Either through kin-recognition or copulating with known females that subsequently fledged their broods, males were able to discern between fledged and failed nests containing their EP offspring.

In order for dispersal decision rules to evolve, the factor affecting their dispersal must be predictable between years. Males that returned to a familiar site were more likely to gain EPFs than those males immigrating into an unfamiliar site. Age, which is often correlated with experience and EP mating success, was no longer important in predicting EPFs after controlling for experience. Experienced males were cuckolded at similar rates to inexperienced males which suggested that quality was not influencing the effect of experience on EPFs. Males returned to areas with more EP mating opportunity and produced more offspring, which is not possible for females in this system. Hence, cuckoldry or EP mating has directly opposite effects on male and female dispersal decisions and conforms nicely to Greenwood's prediction that the prevailing mating system can explain patterns of sex-biased dispersal.

CHAPTER 1 INTRODUCTION

One of the most studied yet least understood facets of life-history is the movement of individuals and genes both among and within populations (Clobert et al. 2001). Dispersal, both natal and breeding, contributes to the mixing of gene pools, the persistence of populations, and the evolution of species. The incentives, causes and consequences of dispersal are considerable evolutionary forces that are governed by social interactions, habitat quality, and ultimately individual fitness.

Sex-biased patterns of natal and breeding dispersal are widespread in the animal world and are likely a result of the prevailing mating system (Greenwood 1980; Greenwood & Harvey 1982); however, identifying the specific factors driving these sex differences has proven difficult. Although natal dispersal is more extensive for long-lived species, breeding dispersal decisions are often made repeatedly throughout the lifetime of an individual. In socially monogamous songbirds, breeding dispersal is female-biased (Clarke et al. 1997), presumably because the male, which is usually the territorial sex, benefits by returning to a familiar location (Greenwood 1980). Breeding habitat quality often varies significantly in space and time and may also vary by sex because of discrete sex roles in reproduction. Hence, there should be strong sex-specific selection on the ability to accurately assess habitat quality. Breeding dispersal decisions and habitat selection have been shown to be influenced by individual reproductive success (IRS) (Switzer 1997; Haas 1998; Hoover 2003) and conspecific reproductive success (public information) (Doligez et al. 2002; Parejo et al. 2007; Boulinier et al. 2008). Typically, both males and females are likely to disperse between years after high reproductive success compared with low or failed reproductive success (i.e., “win-stay,

lose-switch”: Haas 1998; Hoover 2003). Failed breeders, however, must rely on alternative sources of information, such as public information or habitat cues (e.g., food availability, conspecific density, inter-specific competitors etc.) when searching for a new breeding location. Migratory species that have little time to assess habitat quality prior to the end of the breeding season may rely more heavily on public information because it integrates multiple environmental cues that ultimately determine reproductive output (Danchin et al. 2004). If sex-biased dispersal does not tend to vary with IRS, then we might expect adult breeding sex-biased dispersal to arise from sex differences in the use of public information.

Public information has been the focus of intensive research as it relates to dispersal and habitat selection. Few of these studies have fully explored whether the sexes predictably vary in their use of public information. Territorial males may be more attuned to territory- or neighborhood-specific quality because males must select and defend a territory prior to the arrival of other males and females (Kokko et al. 2006). In addition, interactions with neighbors on territorial boundaries can significantly influence male fitness (Beletsky & Orians 1989; Temeles 1994; Akçay et al. 2009) (e.g., costly defensive battles, cuckoldry, extra-pair fertilizations) and should factor into the breeding dispersal decisions of males. Females, however, can return to good patches and choose from males that presumably defend the best territories. In addition, if females do not benefit from territory familiarity as much as males, then they may have evolved to be more dispersive as a means of avoiding recently sampled low quality or incompatible mates. Thus, examining differences in dispersal decisions of unsuccessful (i.e., failed in

their own breeding attempts) males and females offers the best opportunity to identify sex-differences in breeding dispersal and the use of public information.

In my thesis, I generally focused on the between-year breeding dispersal of prothonotary warblers (*Protonotaria citrea*) that were shown previously to exhibit a “win-stay, lose-switch” dispersal strategy. In this species, successful males and females were equally likely to return to their patches between years, whereas unsuccessful birds dispersed (Hoover 2003). In Chapter 2, I examined whether unsuccessful males and females differed in their between-year breeding dispersal and whether different scales (neighborhood vs. patch) of conspecific reproductive success (i.e., public information) could explain the sex-specific patterns of dispersal. I experimentally manipulated the reproductive success of all warbler pairs on discrete patches of bottomland forest habitat. Consequently, reproductive success was not dictated by environmental factors such as predation and/or food availability, which thus eliminated confounding factors such as individual and/or environmental quality that are thought to be associated with dispersal. I examined separately whether males and females based their between-year site fidelity on public information at either the neighborhood (number of successful neighbors) or patch scale (reproductive success in the larger habitat patch). I also explored whether dispersal distances were correlated with the factor that contributed most to the site fidelity of each sex.

After I determined whether public information at different scales could explain sex differences in breeding dispersal, I examined alternative hypotheses for between-year breeding dispersal in males and females separately. In Chapter 3, I examined whether dispersal decisions of unsuccessful males were based on the success of neighbors or

on private information in the form of their own extra-pair (EP) mating success.

Neighborhood success could influence an individual male's own success via EP mating because previous studies from several related species showed that, in general, EP offspring were sired by neighbors (Perreault et al. 1997; Stutchbury 1998; Pedersen et al. 2006). I predicted that unsuccessful males would be more likely to sire and have EP offspring fledge with more successful neighbors. I also expected neighborhood fidelity to be increased for those males with EP mating success compared to those males without EP mating success. I expected those males that failed on all fronts (own nest and EP success) to base dispersal decisions on public information in the form of the number of successful neighbors.

In Chapter 4, I examined whether breeding dispersal decisions in unsuccessful female warblers were related to public information on patch reproductive success (PRS) or on private information in the form of cuckoldry. Cuckoldry is likely an adaptive response to improve offspring quality for females mated to either low quality (i.e., "good genes") or genetically incompatible (i.e., "compatible genes") mates (Akçay & Roughgarden 2007). In general, female birds are thought to be more dispersive as a means of avoiding inbreeding (Greenwood 1980). In species such as the prothonotary warbler, where natal dispersal is not sex-biased nor is it always adequate to eliminate incestuous matings (M. Mckim-Louder in prep.), breeding dispersal in females may be a means of avoiding re-pairing with closely related mates. To avoid the confounding factor of territory quality on dispersal decisions in females I focused on unsuccessful females that were generally surrounded by successful pairs. All females, in theory, were dissatisfied with the quality of their territory; therefore, the majority should at least switch

territories. Because unsuccessful females were generally surrounded by successful pairs in my experiment, they would not necessarily need to disperse outside of the neighborhood to find a good quality territory. However, if females were dissatisfied (i.e., cuckolded) with their former social mate, either because of genetic incompatibility or low quality, then their between-year dispersal should be longer than those not dissatisfied with their former social mate. I examined patterns of cuckoldry and breeding dispersal as they related to female relatedness to her social mate, and social male quality based on male size and heterozygosity. If “good genes” explains cuckoldry in my system then only the best quality males should gain EP fertilizations, versus “compatible genes” where EP offspring would be more evenly distributed among males. In my study system, EP offspring were moderately rare (Chapter 3 & 6) and did not appear to be skewed towards any particular males. Thus, I predicted that female’s relatedness to their social mate would best predict the probability of cuckoldry. I also tested whether between-year site fidelity of unsuccessful females was related to public or private information in the forms of PRS and cuckoldry. I predicted that if females unsuccessful in their own nest cuckolded their mate, they may use this information to indicate the presence of a genetically compatible mate and return to the patch at a higher rate between years than those females that did not sample other males via cuckoldry. I also examined whether between-year dispersal distances of unsuccessful females could be explained by female relatedness to her social mate in the previous year. If females disperse to avoid breeding again with a closely related social mate then their dispersal distances should increase with an increased relatedness to their social mate and be extensive enough to limit interactions with that particular male in the subsequent year.

In Chapter 5, I returned to males to examine how accurately they could gauge their EP mating success. In Chapter 3, I showed that EP mating success, i.e., fledged EP offspring with a neighbor, influenced the between-year neighborhood fidelity of unsuccessful males. What was not known was whether males were aware that their EP offspring fledged from a neighbor's nest, or whether males with EP fertilizations that did not result in a fledged young would respond in the same way. In Chapter 5, I conducted a post-hoc analysis by focusing on successful males that were surrounded by variable numbers of successful neighbors as a result of the manipulations of individual reproductive success during the years of the experiment. Males, therefore, fledged EP offspring only if the EP offspring occurred with a successful neighbor's nest. Therefore, successful males could be placed into three categories: (1) those without any EP mating success, (2) those that sired EP offspring that did not successfully fledge, and (3) those that sired EP offspring that fledged. Category three males that had EP offspring fledge are the only category of males that effectively increased their realized reproductive success. Therefore, if dispersal decisions evolved directly as a response to EP mating success, then the category of males with EP offspring that fledged should be most likely to return to their neighborhood compared to the other two categories.

If male between-year breeding dispersal decisions evolved directly as a result of EP mating success, then gaining EP fertilizations should be somewhat predictable between years (Switzer 1993). Hence, returning to a familiar place between years may give males an advantage if it significantly increases their probability of siring EP offspring. In Chapter 6, I tested this hypothesis using all males that bred on my study sites during my experiment. I examined whether breeding experience on the site in the

previous year, neighborhood size, or age influenced the probability that a male would gain at least one EP fertilization. Because dispersal decisions in males included responding strongly to the fledging of their EP offspring by returning to their neighborhoods between years (Chapter 5), I predicted that returning to a familiar location would increase a male's probability of gaining EPFs compared to those males unfamiliar with a site. I expanded this analysis to include a known-age sub-sample of males to tease apart the importance of male age versus prior breeding experience at a site to gaining EPFs. I also tested whether prior breeding experience or age influenced first clutch dates and the size of their neighborhood in which they bred. Previous experience on the site may give males an advantage by allowing them to settle first, while also knowing in advance where the best neighborhoods will be. I also examined whether previous breeding experience decreased the probability of being cuckolded by their mate to determine whether gaining EPFs was offset by the loss of paternity within their own nest.

CHAPTER 2
PUBLIC INFORMATION COLLECTED AT SEX-SPECIFIC SPATIAL SCALES
EXPLAINS FEMALE-BIASED BREEDING DISPERSAL

Introduction

Dispersal has profound effects on population dynamics and evolutionary processes of species yet our understanding of this complex behavior is incomplete (Clobert et al. 2001; Clobert et al. 2009). Both sex-biased natal and breeding dispersal are widespread phenomena thought to be best predicted by mating systems (Greenwood 1980; Greenwood & Harvey 1982); however, identifying the specific factors driving these sex differences has proven difficult. Although natal dispersal is typically more extensive, for long-lived species breeding dispersal decisions comprise the majority of dispersal events throughout the lifetime of an individual.

The quality of breeding habitat strongly influences the fitness of individuals. For many species, habitat quality varies both in space and time; thus, there is strong selection on individuals to make optimal dispersal decisions. Males and females are often assumed to respond similarly to information in the environment that might provide a means to assess habitat quality (Muller et al. 1997; Murphy 2001; Doligez et al. 2002; Betts et al. 2008; Redmond et al. 2009) and in some cases, they seem to use the same cues (Switzer 1997; Haas 1998; Doligez et al. 2002; Hoover 2003a). Because males and females of most organisms often differ in their tendencies to disperse, however, we might expect that they use different information or respond to the same information differently. In birds, in particular, males are less likely to disperse than females (Greenwood & Harvey 1982; Clarke et al. 1997). This pattern of sex-biased breeding dispersal in birds leads to the prediction that males and females may use information gathered at different scales when making dispersal decisions.

Studies of long-lived species that breed for many years have shown that individuals are more likely to return to breed in a particular location where they have produced offspring and this “win-stay” strategy has been demonstrated for many species (Wauters et al. 1995; Switzer 1997; Haas 1998; Hoover 2003a; Citta & Lindberg 2007). Breeding failures can also inform individuals about habitat quality and typically result in dispersal away from bad habitats (i.e., “lose-switch”) (Switzer 1997). Breeding failures provide information about where not to breed but provide no information about where to breed in the future. Failed breeders often comprise the majority of dispersing individuals and therefore their decisions to disperse can have a strong influence on local population dynamics (Clobert et al. 2001). Information from the environment (e.g., food availability, predator abundance) (Lin et al. 2006) and/or conspecifics (e.g., conspecific density, patch reproductive success) (Danchin et al. 2001) may be particularly important to failed breeders because it can inform them prior to choosing subsequent breeding locations. Information gleaned from conspecific reproductive success (i.e., public information) may be the most informative because it integrates the many factors governing individual reproductive success (e.g., the presence of mates, nest sites, ample food, and low rates of nest predation and parasites) (Schjorring et al. 1999; Danchin et al. 2001; Doligez et al. 2002; Valone & Templeton 2002; Doligez et al. 2003; Boulinier et al. 2008; Redmond et al. 2009).

Past research on public information has focused on the effects of both the number and quality of conspecific offspring on breeding dispersal, but has typically ignored any possible sex differences in the use of this information (Doligez et al. 2002; Parejo et al. 2007). The exact scale at which dispersers collect public information is not well known

(Boulinier et al. 1996; Pärt & Doligez 2003; Doligez et al. 2004; Dittmann et al. 2007).

The majority of studies that examined the use of public information used patch reproductive success (PRS) (the average number of offspring/female/patch/year) of conspecifics; however, few have attempted to simultaneously examine sex-specific differences at more than one spatial scale (but see Doligez et al. 1999; Citta & Lindberg 2007).

In birds, males typically defend the territory (Lack 1968) and for migratory species, males arrive first on the breeding grounds (Coppack et al. 2006; Kokko et al. 2006). Hence, males may collect more territory-specific information about habitat quality, whereas females may simply return to good patches and choose the best mate or assume that males occupy the best territories first. In addition, benefits may accrue for males, the territory defenders, if they return to familiar areas and these benefits may be less relevant to females. For example, males in neighborhoods with familiar neighbors likely spend less time defending their territorial borders (Eason & Hannon 1994; Temeles 1994; Frostman & Sherman 2004; Akçay et al. 2009). These sex-specific factors may lead to sex-specific interpretations of habitat quality.

For unsuccessful breeders, in particular, the amount of time available for prospecting in the season is potentially limited and may vary by sex. Because males and females differ significantly in their breeding roles (Greenwood 1980) we might expect sex-specific temporal and/or spatial constraints on their ability to collect public information during the breeding season. Females are typically tied to the nest during the majority of the breeding season while they alone build their nest and incubate their eggs (Petit 1999), whereas males are free to observe and interact with neighbors. Females

may have opportunities to prospect only after their last breeding attempt when successful conspecifics are mostly feeding fledglings and are no longer tied to particular territories, which would only allow for a patch-wide assessment of habitat quality. Thus, it becomes important to examine the use of public information at both the scale of the neighborhood and the patch.

The identity of prospectors, those assumed to be collecting public information, is typically unknown [but see (Ottoesson et al. 2001)], and the extent of their knowledge or experiences is often assumed (Pärt & Doligez 2003; Doligez et al. 2004). To understand if sex differences exist in the use of public information it becomes important to know their location prior to dispersing and the type of information available to them. By focusing on failed breeders of known origin I can examine whether sex differences arise in the use of public information. Few studies have attempted to distinguish how information at different spatial scales influences site fidelity (returning between years to the same patch of breeding habitat) and breeding dispersal of failed breeders (but see Doligez et al. 1999). None, to date, have manipulated experimentally the reproductive success of conspecifics at multiple spatial scales to test for an effect of neighborhood and patch reproductive success on site fidelity and dispersal of failed breeders.

Prior experiments in this study system showed that between-year site fidelity increased with an increase in individual reproductive success (i.e., 0, 1 or 2 broods fledged) in both male and female prothonotary warblers (*Protonotaria citrea*) (Hoover 2003a). Unsuccessful individuals returned to their patch between years at a relatively low rate suggesting that the “win-stay/lose-switch” strategy was operating in this system and was effective because of both the spatial and temporal predictability of territory

quality. Among unsuccessful individuals, males were more than twice as likely as females to return to their patch (Hoover 2003a). A further investigation of this pattern revealed that unsuccessful males with at least one successful neighbor were more likely to return to their patch than males without any successful neighbors. In contrast, the success of neighbors did not affect unsuccessful females and unsuccessful females that returned to their patch were more likely than males to disperse away from their previous territories (Hoover 2003a). These results suggested an influence of neighborhood quality on the site and neighborhood fidelity of unsuccessful males and potentially an influence of a larger scale of public information, such as PRS, on females.

Here I experimentally examined the effect of public information on site and neighborhood fidelity (i.e., breeding dispersal) of unsuccessful prothonotary warblers. I focused on the between-year movements of individually marked warblers in relation to neighborhood reproductive success, PRS, and conspecific density. Specifically, I experimentally induced reproductive failure of focal pairs and manipulated neighborhood quality by varying the number of successful neighbors. By manipulating reproductive success of individual pairs, I also indirectly manipulated PRS. I examined only the smallest and largest spatial scale to eliminate confounds based on spatial autocorrelation of nesting success. Because previous research showed an effect of neighbor success on unsuccessful males and not unsuccessful females (Hoover 2003a), I predicted that the site fidelity of unsuccessful male warblers would increase and dispersal distances decrease with an increase in the number of successful neighbors. For unsuccessful females, I predicted that higher PRS, and not neighbor success, would result in higher site fidelity and reduced dispersal, because of the

female-specific temporal and spatial constraints that likely affect their ability to collect public information during the breeding season.

Materials and Methods

Study Area and Study Organism

I conducted this research within the Cache River Watershed in Illinois, USA (37° 18' N, 88° 58' W). The Cache River has a total length of 176 km and meanders through the southern tip of Illinois to the Ohio River, draining 1,537 km² of land (Mankowski 1997). I chose eight study sites that were discrete patches of forested wetland habitat in a landscape primarily consisting of bottomland forest (9% of land cover), upland forest (26%), agriculture (32%), and grassland and successional habitat (31%) (Mankowski 1997). These study sites (area range, 8 to 73 ha) were separated from each other by at least one kilometer of habitat not suitable for breeding prothonotary warblers (e.g., upland forests, agriculture, or successional habitat).

The prothonotary warbler is a migratory songbird that winters in the Neotropics and breeds in the central and eastern United States (Petit 1999). This species is territorial and socially monogamous (Petit & Petit 1996), nests in secondary cavities, and associates closely with standing water in bottomland and swamp forests (Petit 1999). Prothonotary warblers prefer to nest over water (Petit & Petit 1996) and readily use nest boxes (Petit 1989; Blem & Blem 1994; Hoover 2003a), which have been shown to yield similar nest predation rates and warbler densities as natural cavities (Hoover 2001). Prothonotary warblers are capable of producing up to three broods in a year, but the majority produces one or two broods. Additional details of the warbler's natural history and behavior are given elsewhere (Petit 1999; Hoover 2003b, 2006).

Prothonotary warblers are ideally suited for testing the neighborhood hypothesis as it relates to between-year fidelity to patches of breeding habitat (site fidelity hereafter) and local dispersal because: (1) they are restricted to a particular habitat type, which simplifies the process of relocating site faithful and dispersed birds; (2) they are easy to capture, individually color-mark, and follow for an entire breeding season (Hoover 2003a); (3) they use nest boxes, allowing me to experimentally manipulate the nesting success of individual pairs of birds; and (4) it was previously demonstrated experimentally that site fidelity of individual males and females is based on decision rules and is lowest for those that are unsuccessful and increases with the number of broods (1 or 2) successfully fledged (Hoover 2003a). Here I study factors associated with sex-specific variation in the site and neighborhood fidelity and dispersal of unsuccessful individuals, that is, those that fledge no broods the previous year.

Monitoring Individuals and Manipulating Nesting Success

From 1996 to 2005 I monitored breeding populations of prothonotary warblers that used nest boxes made from modified 1.9-L cardboard milk and juice cartons (Fleming & Petit 1986). Nest boxes were attached to trees and placed on study sites in a grid formation with 35 to 50 m spacing between boxes that covered each of the eight study sites. Each study site had at least eight breeding pairs of warblers each year. Each year, only a portion of the nest boxes were used on a given. Overall, the percentage of nest boxes occupied on each site, each year, ranged from 16 to 53 % ($33.9 \pm 11.5\%$; mean \pm SD, $n = 12$).

I captured all individual warblers on study sites every year and color-marked each male and female with a unique combination of a numbered aluminum and colored plastic leg bands. I measured and recorded wing chord (mm), tarsus (mm), tail length

(mm) and mass (g) for all adults captured. Males were captured in mist nets by placing a decoy of a male warbler in front of a mist net within the territory of the male while playing a recording of a male prothonotary warbler song. I captured females by placing a small plastic bag over the openings of nest boxes containing females that were incubating eggs. On these study sites I knew the identity of the male and female associated with every nesting attempt each year. Adults were aged as either second-year (SY: one year old) or after second-year (ASY: more than one year old) based on plumage (Pyle 2001) and morphometric characteristics (unpublished data J. Hoover).

I experimentally manipulated the nesting success of individual pairs on each study site. During each year from 1996 to 2001, I randomly assigned one of two experimental treatments to pairs so that approximately 60 to 70% failed to fledge offspring and the remainder successfully reproduced on each site (similar to natural levels of reproductive output (Hoover 2001)). The nest boxes used by pairs in the “failure” treatment group remained attached to trees and nest predation prevented these birds from producing any fledged offspring regardless of how many broods were attempted. Nest boxes used by pairs in the “success” treatment group were removed from trees and reattached to two pieces of 1.50-cm-diameter greased conduit placed in the ground and standing one meter away from the original nest tree. Nest boxes placed on conduit were safe from nest predation.

During 2002-2004, on four of the study sites (area range, 10 to 44 ha) I continued the manipulations of nesting success described above but changed the proportion of pairs that were unsuccessful to 33% for the purpose of a different experiment. On these

sites I placed the nest boxes used by every pair on greased conduit as boxes became occupied. I then manipulated all nesting attempts of particular pairs (failure treatment) to simulate nest predation and prevent them from fledging any nestlings. Unsuccessful pairs were chosen so that, subsequent to these manipulations, they were surrounded by mostly successful neighbors (pairs in adjacent territories). For each nesting attempt of these unsuccessful pairs I removed nestlings when they were 4 to 6 days old (they fledge on day 11) and pulled some of the nesting material into the opening of the nest box to mimic nest predation by a raccoon (*Procyon lotor*), the prominent nest predator in the system (Hoover 2006). I relocated all nestlings to foster parents on other sites not included in the experiment where they were raised under natural levels of nest predation. The pairs of warblers in the unsuccessful treatment group failed to fledge any offspring during the entire breeding season.

I monitored all nesting activity of each individual on every study site (see Hoover 2003a for detailed monitoring protocol) and recorded the number of warbler offspring produced by each nesting attempt. At the end of each breeding season I had complete information on the identity and reproductive output (warbler offspring fledged) of all prothonotary warblers breeding on my study sites. Individuals that were assigned to the failure treatment group in one year were never re-assigned to fail in a subsequent year. Therefore my sample sizes represent the total number of individual males and females that were unsuccessful, and their site fidelity and local dispersal in the year after assignment to the failure treatment. Because each individual was used only the first time they were assigned to a treatment group, the male and female from each pair was not always included in the total sample. During 1996 to 2001 treatments were assigned

at random; because males are generally less dispersive than females, I ended up with fewer individual males overall. During 2002 to 2004, unsuccessful pairs were randomly selected from the sub-sample of males that had not been previously unsuccessful for the purposes of another experiment. Consequently, during 2002 to 2004, male and female sample sizes were nearly equal.

I recorded the number of successful neighbors for each focal pair. Neighbors were defined as warbler pairs with territories adjacent to the focal pair and limited to a radius of three nest boxes (~160 m) in all directions, which constituted approximately one territory deep beyond the focal pair. I documented patch reproductive success (PRS; average number of warbler offspring produced per female per year on a given study site) and estimated the density of breeding pairs of warblers (conspecific density; number of breeding females divided by total area of breeding habitat) on each study site each year.

Documenting Site Fidelity and Local Breeding Dispersal

Within each study site I determined the identity of every color-marked individual returning from the previous year and captured and color-marked any new individuals that were not banded. For the purposes of this paper, I focused on the returns of those males and females that failed to fledge any offspring from their own nest in the previous year. I determined whether or not unsuccessful individuals returned to study sites the following breeding season and searched for any dispersing color-marked birds within a 500-m wide area surrounding each study site. I estimated distance moved for those individuals that returned by measuring the distance (to the nearest 5 m) between the approximate centers of the territories (based on the locations of nest boxes used) they occupied during the previous and current year. During the years of my study breeding

densities on patches did not reach saturation (population densities increased every year) and were unlikely to affect an individual's ability to remain patch faithful.

Statistical Analyses

Multi-year ecological studies are inherently riddled with confounding effects of study sites and annual variation and other random factors that are not central to the question of interest. Generalized linear mixed models (GLMMs) are appropriate tools that allow for control of these various random factors (Bolker et al. 2009). Random effects can include blocked data according to sample unit or residual variation as a result of random ecological factors (e.g., annual effects on food, rainfall etc.). In addition, GLMMs are a multivariate model used for the analysis of non-normally distributed response variables.

I used generalized linear mixed models (GLMMs) using GLIMMIX procedures in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) with a binomial error distribution (response variable coded as "0" and "1") and a logit-link function to model the probability of individual return to a patch. Because the penalized quasi-likelihood (PQL) method, the default in SAS, can be biased for binary data I used the Laplace approximation method for approximating the likelihood (Bolker et al. 2009). To determine if disturbing the pairs by moving nest boxes off of trees onto greased conduit had an unintended influence on the returns of males and females to their patch I used a subset of data from 2003 and 2004. During these two years, I had the most variation in whether boxes were already on poles (no disturbance) or whether they still had to be moved from the tree to greased conduit (disturbance). I constructed a GLMM using a total of 125 individuals with the sexes combined (males: $n = 68$, females: $n = 57$) to examine the influence of box disturbance (yes, no), sex and the interaction between box disturbance and sex on

between-year return to the site (yes, no). I included the identity of the patch as a blocked random effect. I found no evidence that either box disturbance (GLMM; $\beta = -0.62 \pm 0.85$, $F_{1,109} = 0.54$, $p = 0.463$) or the interaction between sex and box disturbance (GLMM; $\beta = -0.34 \pm 0.53$, $F_{1,110} = 0.54$, $p = 0.521$) had any unintended influence on individual site fidelity.

To determine whether my experiment influenced the return of unsuccessful birds to the patch in ways that are similar to others that have examined the use of public information, I first constructed a GLMM using all unsuccessful males and females combined ($n = 429$) to examine the influence of PRS and sex on the probability of return to the patch. Most other studies that have examined dispersal decisions in relation to public information have pooled data from both sexes and examined only the patch-scale of conspecific reproductive success. I included patch conspecific density (pairs/ha) and patch area (ha) in my model to control for any confounding influences of the patch. I also included patch identity and year as random effects to control for non-independence of observations or patch-specific conditions that may systematically bias individual returns (e.g., patch isolation, food availability, parasites etc.). Individuals were used only once in my experiment. For all GLMMs I evaluated the importance of fixed effects using Wald-type statistics reported by the GLIMMIX procedure in SAS. Beginning with a full model that included all fixed effects I used a backward stepwise approach by progressively eliminating non-significant variables ($\alpha = 0.05$). Variables with p-values less than 0.10 were retained in the final model. The non-significance of removed variables was confirmed by adding them to the final model. PRS (0.60 to

7.08 offspring/pair) and conspecific density (0.41 to 2.00 pairs/ha) and area (8 to 73.0 ha) were used as scale variables.

To examine whether the spatial scale or type of public information used differed based on sex I analyzed each sex separately (males $n = 220$, females $n = 209$) and included both the number of successful neighbors, PRS, and patch conspecific density as fixed effects and site and year as random effects. I also included age, coded as a binary variable representing SY or ASY respectively, because age has been shown to influence adult breeding dispersal in other species (Winkler et al. 2004; Eeva et al. 2008).

I placed all unsuccessful individuals known to have returned between years into one of two categories based on their return locations (same territory or neighborhood vs. outside of neighborhood on same or different habitat patch) and used a chi-square analysis to test for differences between males and females between categories. To evaluate sex differences in overall distance moved of the birds known to have returned I used a GLMM with a Gamma distribution and log-link function using PQL to approximate the likelihood where sex was the fixed effect and site was a random effect. The Gamma distribution is a positively skewed distribution with values greater than but not equal to zero. To include all individuals (males $n = 105$, females $n = 73$) in the analysis I added five meters to all distances so that individuals that returned to their former nest-box would have a non-zero value. For each sex, I also used a GLMM using a Gamma distribution with a log-link function to test the prediction that local movements (of all returning unsuccessful birds) would be affected by the factor having the greatest effect on site fidelity. For all GLMMs for local movement analyses I used the

Kenward-Roger adjustment for calculating the degrees of freedom (Kenward & Roger 1997). The Kenward-Roger adjustment is more robust than SAS defaults methods for small sample sizes and uneven block designs (Kenward & Roger 1997; Kowalchuk et al. 2004).

Results

Totals of 220 males 209 females were in the failure treatment group and 155 males and 249 females were in the success treatment group. Overall, 192 males (51%) and 198 females (43%) returned between years to their previously used habitat patch. Both males and females in the success treatment group were more likely to return to their patch between years than birds in the failure treatment group [males (success vs. failure), 60 vs. 45%; chi-square; $X^2_1 = 7.03$, $p < 0.008$; females, 55 vs. 29%; $X^2_1 = 33.04$, $p < 0.0001$].

With the sexes combined, PRS (patch-wide average number of offspring per female per year) and sex best explained the probability of unsuccessful individuals returning to the patch with males being more patch faithful than females (Table 2-1, Figure 2-1). Upon closer examination of the sexes, when the additional variable representing public information available at the neighborhood spatial scale (the number of successful neighbors) was included in analyses, I found that the number of successful neighbors was the variable that now best explained site fidelity in males (Table 2-2) whereas PRS still best explained female site fidelity (Table 2-3). Site fidelity in males increased with number of successful neighbors (Figure 2-2). Female site fidelity increased with increasing PRS (Figure 2-3). Age was not correlated with the number of successful neighbors for males (Pearson's $r = -0.008$, $n = 220$, $p = 0.983$) nor PRS for females (Pearson's $r = 0.018$, $n = 209$, $p = 0.797$).

Totals of 105 unsuccessful males and 73 unsuccessful females returned to the study area between years (those returning to patches plus those switching patches). Overall, local movements of those males were significantly shorter than females (GLMM; $F_{1,175} = 27.88$, $p < 0.0001$, Figure 2-4). Males were more likely than females to return to locations within their previous neighborhood (including their previous territory) whereas females returned more than males to locations outside of their previous neighborhood ($\chi^2_1 = 14.24$, $p < 0.0001$; Figure 2-5). Of the five males that moved to a different habitat patch between years, three had no successful neighbors and two had one. Females ($n = 13$) that switched habitat patches between years did so after breeding on sites with low PRS (mean \pm 1 SE = 0.87 \pm 0.22 offspring/female/patch/year) compared to females ($n = 60$) that did not switch (3.37 \pm 0.22; two-tailed $t_{39} = -7.94$, $p < 0.0001$, unequal variances).

Because the number of actual and successful neighbors was positively correlated and male-male competition may lead to non-random sorting of quality of individual males (Petit & Petit 1996) I wanted to make sure that higher return rates of males in larger neighborhoods was not an artifact of male quality. To examine this I looked at all males that had one successful neighbor and compared within this group whether the actual number of neighbors positively increased return rates. I chose one successful neighbor because this group was represented with the largest sample of males ($n = 45$) and because I had nearly the full range of actual neighbors (range = 1 to 4) to test for the effect. In this case, the number of actual neighbors (i.e., neighborhood density) did not increase return rates of males (Pearson's $r = -0.167$, $p = 0.329$).

Local movements of all unsuccessful returning males ($n = 105$) to the study area decreased with an increase in number of successful neighbors (GLMM; $\beta = -0.19$, $F_{1,85} = 7.38$, $p < 0.0001$, Figure 2-6). Local movements of all returning females ($n = 73$) was negatively correlated with PRS (GLMM; $\beta = -0.28$, $F_{1,71} = 8.72$, $p = 0.003$, Figure 2-7) regardless of age ($\beta = 0.30$, $F_{1,70} = 0.69$, $p = 0.50$).

Discussion

In this study, I experimentally determined that the reproductive success of conspecifics positively influenced patch fidelity of unsuccessful male and female breeders. By randomly selecting unsuccessful pairs, the group most likely to disperse (Switzer 1997; Haas 1998; Hoover 2003a), I reduced and/or eliminated confounding factors such as individual quality and age, and habitat cues such as food availability and predator abundance, that are sometimes correlated with reproductive success (Lemon et al. 1996; Lurz et al. 1997; Morrison & Bolger 2002; Kim & Monaghan 2005). Because I had previous evidence from this system that unsuccessful males returned at a higher rate when they had at least one successful neighbor (Hoover 2003a) I examined the influence of neighbor reproductive success, PRS, and conspecific density in year x on neighborhood and patch fidelity of individual males and females separately in year $x+1$. I found evidence that males and females differed in the scale of public information that they used to decide where to breed in the subsequent season. Males only responded to the number of successful neighbors, whereas females only responded to PRS. Between-year patch fidelity of failed breeders increased with the number of successful neighbors for males, but with PRS for females. Dispersal distances of the failed breeders that returned decreased with the number of successful neighbors for males, and with PRS for females, corroborating the effect of neighbor reproductive success on

male returns and PRS on female returns. Males were more likely than females to return to their neighborhood and females were more likely to switch patches, even when controlling for possible effects of male quality. Thus my experiment demonstrated sex differences in the use of social cues to assess habitat quality. In the rest of the discussion, I illustrate how these patterns could arise and explore why females are more dispersive in this species.

This is the first experimental study, to my knowledge, that demonstrates a sex difference in the scale at which public information is used. There have been only a handful of previous studies that have looked at different scales of public information and sex differences simultaneously. The study with the result most similar to mine examined the post-breeding movements and between-year site shifts of northern wheatears (*Oenanthe oenante* L.) (Arlt & Pärt 2008b), which found that males returned to breeding sites based on high neighbor success and were more likely to shift to new sites when both density and neighbor success were low. In contrast, females typically moved from their former breeding site based not on public information, but rather their own reproductive success. The authors did not, however, examine the possible role of public information at a scale larger than the neighborhood, which may have helped explain what information females used in their dispersal decisions beyond their own reproductive success. A correlative study of collared flycatchers (*Ficedula albicollis*) (Doligez et al. 1999) indicated that dispersal of unsuccessful females was negatively related to all scales (continuous levels ranging from the neighborhood to the patch) of local reproductive success in their study, a result similar to this study. Unsuccessful males, however, were actually more likely to leave the best patches based on only the

largest patch-wide scales of public information, which contrasts with my findings. Doligez et al. (1999) suggested that the low quality of failed male breeders likely influenced movement of these individuals from high quality patches to lower density patches where they could better compete for multiple females (Doligez et al. 1999). In Doligez et al.'s study, only 13% of the birds failed to produce offspring and only eight of 39 individuals switched patches, which the authors admitted gave them little statistical and explanatory power.

Ward & Weatherhead (2005) found sex differences in the type of information used to decide whether to disperse in the polygynous marsh-nesting yellow-headed blackbird (*Xanthocephalus xanthocephalus*). Females used PRS whereas males were more likely to use their own harem size (degree of polygyny), which could be related to neighborhood quality. They did not, however, explore public information at a scale finer than PRS (Ward & Weatherhead 2005). Redmond et al. (2009) examined different scales of social cues including PRS and conspecific density on eastern kingbirds and found that conspecific success at their smallest scale (200 m) was the only scale significant in determining where birds dispersed to. In their analyses, they combined sexes even though they found differences in dispersal distances for males and females. Although these studies examined different scales of public information and/or sex differences in the type of information used, they did not control for other confounding factors such as individual quality, information pertaining to individual reproductive success, or habitat variation. Nevertheless, there is evidence that males and females of other species sometimes differ in either the scale or type of public information used.

Public Information and Constraints on Prospecting

Little is known about when and where public information is gathered and even less is known about which specific cues individuals use to assess habitat quality (e. g. conspecific density, nestling and/or fledgling number and/or quality, parental activity) because most of these cues tend to be correlated (but see Doligez et al. 2002). It is likely that multiple cues are used depending on individual experience (naïve vs. experienced and successful vs. failed breeders), causes of reproductive failure (predators, parasites, food availability, parental quality), and individual competitive ability (Doligez et al. 2002). Unsuccessful breeders are one of the most likely groups to prospect given that they do not have sufficient information from their own past breeding experience to select a good territory. I did not collect information on prospecting to know whether the sexes differ in this behavior. Nevertheless, in this study, I found that unsuccessful males and females used different scales of conspecific success or a correlated factor to influence their dispersal. I suspect, therefore, that unsuccessful males may have more opportunity to prospect in their immediate neighborhoods while defending their territory, whereas females may be more constrained during the breeding season while they are tending their clutches and broods.

The sexes may differ in the type of public information they use to assess patch quality depending on the time (during breeding vs. post-breeding) and/or location that information is gathered. Sex roles may place different spatial constraints on an individual's ability to collect information. During the breeding season, males actively defend territories and may be unwilling to venture far from their neighborhood (Westneat 1993). Females may foray farther looking for food resources and potentially prospecting, but are likely limited to a small window of time during their fertile period

prior to egg-laying. In studies that have looked for differences in foray behavior between males and females, however, no clear pattern has emerged. Pedersen et al. (2006) documented that the foray rates of male and female common yellowthroats (*Geothlypis trichas*) did not differ and both sexes primarily visited neighboring territories. The only sex difference found was that female yellowthroats limited their foraying to their fertile period prior to egg-laying and forays were associated with extra-pair copulations. In the wood thrush (*Hylocichla mustelina*), females, when alone, tended to foray farther than males, but these forays happened only during the fertile period, which in this species was synchronous, suggesting also that these forays were for extra-pair mating opportunities (Evans et al. 2008). In contrast, longer-distance foray behavior of unsuccessful breeding thrushes, presumably for prospecting, did not differ between the sexes. If female prothonotary warblers do have more opportunity to foray farther during egg-laying, they are either likely accompanied by their mate or information from conspecifics may be unavailable due to relatively high temporal correlation of laying dates within patches. Therefore, it seems unlikely that sex differences in prospecting behavior during the breeding season would sufficiently explain the sex differences in dispersal.

Sex roles could constrain the sexes to prospect at different times of the breeding season. Males may be free to prospect in neighboring territories during the breeding season; whereas females, which are busy with nest-building, egg-laying and incubation may be constrained to collect information post-breeding when they are less tied to duties at the nest. If this is the case, then post-breeding movements of fledged families and fledglings may make it so that the only information available to females is the patch

scale of conspecific reproductive success. Males, in contrast may be more finely attuned to their neighbors, which they have been monitoring throughout the entire breeding season. Studies that have examined prospecting behavior in territorial species have shown that, in general, males were more likely to be seen prospecting and specifically seen looking into the nests of successful breeders whereas females were rarely seen prospecting at active nests (Ottoosson et al. 2001; Pärt & Doligez 2003; Doligez et al. 2004; Dittmann et al. 2007). This suggests that females may gather information during the post-breeding period or pay attention to parental activity or fledglings on the patch. In prothonotary warblers, males typically provide the majority of fledgling care while females are re-nesting or refueling in preparation to nest again (Hoover 2001). In unsuccessful pairs, however, males would be freed from this responsibility and have even more time to obtain information from their neighborhood during the breeding season while females build their next nest and attempt to relay a new clutch with fewer prospecting opportunities to collect public information.

An alternative explanation for the sex difference in the use of public information is that males are more spatially restricted than females in their post-breeding prospecting behavior. During the years of my study, unsuccessful pairs finished breeding on average 16 days sooner (paired t-test; $t_{25} = -10.76$, $n = 26$; $p < 0.0001$; unsuccessful pair mean \pm 1 SE Julian day of last attempt = 176.5 ± 1.7 , successful pairs = 192.5 ± 1.4) than successful pairs on the same site which would allow equal opportunity for both unsuccessful males and females to prospect during the nestling/fledgling phase of successful pairs. Arlt & Pärt (2008a) found that northern wheatear females were more dispersive than males, but the probability of post-breeding

site shifts (i.e., prospecting) did not differ between the sexes. In contrast, males responded to neighbor success when deciding to return to a prospected area in the next year, whereas females did not respond to public information at the scale that they measured. This suggests that although the sexes had similar information available to them, they seemed to respond to it in different ways. Therefore, it seems more likely that males and females have similar opportunity to obtain information at the patch scale, but that males have additional information from the neighborhood they can use that is less available to females. Radio-tracking data from male and female warblers would be necessary to confirm sex differences in prospecting behavior.

Phenological differences in the arrival of males and females at the beginning of the breeding season may also influence the use and availability of public information. Experienced males and females arrive on the site before most young and inexperienced males (Kokko et al. 2006). Because experienced males arrive first and must select and defend territories prior to the arrival of most conspecifics they must rely on their own experience to select from the entire pool of available breeding sites (i.e., good and bad) (Lozano et al. 1996). Females, in contrast, must select from experienced males already defending territories and therefore have a higher probability of selecting a good breeding site (i.e., mostly good). So, although the sexes seem to have similar opportunity to collect public information in the previous year, males are likely to experience stronger selection than females on collecting accurate information of territory- or neighborhood-specific quality, whereas females that pay attention to good patches will likely select a good territory from those already occupied by experienced returning males.

Potential Benefits of Familiarity with Territories and Neighbors

Males may benefit more from a familiar territory or neighborhood than females. Greenwood (1980) suggested that familiarity with food, nest sites and refuges would benefit the sex responsible for maintaining the territory, but these benefits should potentially benefit both sexes equally (but see Piper et al. 2008). In prothonotary warblers, males find available cavities and claim them by adding bits of moss. Males show females a number of cavities before she finally selects the nest location. Because nest-site selection involves both sexes, it is unlikely that males would benefit more than females from familiarity with their territory. Substantial evidence exists that males familiar with a territory are better at acquiring and maintaining it against male competitors (Stamps 1987; Pärt 1995; Takeuchi & Honda 2009), which could result in higher and earlier mating probability (Pärt 1994; Lozano et al. 1996). In good neighborhoods males are more likely to encounter familiar neighbors, which may reduce the energy necessary to defend a territory (Frostman & Sherman 2004; Schwartz et al. 2007). Unsuccessful males were more likely to return to their neighborhoods than females; however, given the predictability of the habitat (Hoover 2003a) an unsuccessful territory is likely to be unsuccessful again thus settling for the territory even though other benefits may accrue via familiarity does not increase one's fitness due the overriding effect of nest predation. Thus territory familiarity alone does not explain why males would settle for their previous year's bad territory.

Males could be returning to good neighborhoods where they can trade up to a better territory in the event a successful neighboring male does not return, which would still provide benefits of familiar neighbors. Of the 84 males that returned to their neighborhood 47% settled for their formerly unsuccessful territory and failed to improve

their situation by obtaining a previously successful territory. Females could adopt this same strategy; however, males can make the “best of a bad job” and gain extra-pair paternity in a good neighborhood and be successful whereas females, in this system, do not gain offspring via conspecific brood parasitism (Chapter 2). Males may actually be returning as a result of their own success via extra-pair fertilizations whereas females are still adopting the “lose-switch” strategy. In recent decades an enormous literature has been published showing that many species of socially monogamous birds (those that typically exhibit female-biased dispersal) seek extra-pair fertilizations (see Akçay & Roughgarden 2007 and the references therein). In several closely related warbler species, males typically sired extra-pair offspring with neighbors (Yezerinac et al. 1995; Stutchbury 1998; Norris & Stutchbury 2001; Pedersen et al. 2006). In prothonotary warblers, 80% of successful males and females return to the patch and, in this category, males and females are equally likely to return to their territory; hence successful neighborhoods are likely to remain intact between years (Hoover 2003a). Although mixed results exist regarding the effect of density on rates of extra-pair fertilizations (Westneat & Sherman 1997), there could be increased opportunities for males in larger neighborhoods. Knowing that good neighborhoods will largely remain intact between years could directly benefit males and not females. Half of the time males can trade up to one of the “successful” territories and the other half may simply produce offspring via extra-pair fertilizations. Breeding experience and/or familiarity with neighbors may enhance this interaction (Beletsky & Orians 1989, 1991; Pedersen et al. 2006). Studies of site fidelity in relation to extra-pair mating success of males (Chapter 3) would provide a test for this hypothesis.

Other Factors

Inbreeding avoidance via dispersal by the non-territorial sex has long been the explanation for why females are generally the more dispersive sex in birds (Lambin et al. 2001; Gros et al. 2008), but only if males benefit more from a familiar territory. Sex-biased natal dispersal and not breeding dispersal, however, is thought to be the behavior that reduces the probability of mating with close relatives (Greenwood & Harvey 1982; Perrin & Mazalov 2000). Recent evidence suggests that either extra-pair copulations or adult breeding dispersal may be alternative methods of reducing inbreeding risk (Daniels & Walters 2000; Cockburn et al. 2003; Foerster et al. 2006; Freeman-Gallant et al. 2006; Wheelwright et al. 2006; Hoffman et al. 2007; Cohan et al. 2008; Fossoy et al. 2008). I have not examined my study population for the incidence or effects of inbreeding and therefore I cannot rule out inbreeding avoidance as a factor influencing female dispersal. Genetic data and detailed pedigree analyses would be necessary to determine whether individuals mate with close relatives and whether females disperse in response to those pairings.

It is possible that females are more dispersive than males simply because males have more available territories from which to choose than females given that females are constrained to settle on only those territories occupied by unmated males (Arlt & Pärt 2008a). Thus, females could be more likely to switch territories and/or patches because of territory availability (number of unmated males present) which is potentially negatively correlated with PRS. I did not collect data on settlement patterns and arrival times during the experiment so a direct comparison between the availability of territories for males and females is not possible. Based on first clutch dates, however, I can infer whether a female's former territory was occupied prior to her arrival or if that territory

was never occupied in the next breeding season to determine whether a territory was available. To test for an effect of territory availability on return rates and dispersal distances on females I categorized the availability of a female's former territory in the next year. I made the assumption that a female's first clutch date was correlated with her arrival time. If a given female's first clutch date preceded the date on her former territory then her former territory was deemed available. If the territory was never occupied in the next year or the occupant's first clutch date was earlier then I considered the former territory to be unavailable. If females are dispersing because of the unavailability of their former territories then I would expect to see a reduction in site fidelity or an increase in dispersal distance with reduced availability. Adding territory availability to the models for site fidelity and dispersal distances in females did not influence the final outcome. In both cases, site fidelity and dispersal distance were still best explained by PRS and territory availability was not a significant factor (GLMM; territory fidelity, $F_{1,52} = 0.26$ $p = 0.61$; dispersal distance, $F_{1,68} = 0.49$ $p = 0.48$).

Conclusions

I showed experimentally that the scale of conspecific reproductive success differentially influenced dispersal of the sexes. The fact that unsuccessful breeders likely constitute the majority of adult breeding dispersal events in birds makes it likely that this group alone may account for sex-biased breeding dispersal in many populations and demonstrates the need to understand fully the mechanisms controlling the use of public information. Further studies are needed to examine the effects of different scales of public information on the sexes. Additionally, detailed studies on sex differences in prospecting behavior, benefits of familiarity, and patterns of extra-pair

fertilizations and inbreeding are needed to discriminate between the potential proximate mechanisms that influence dispersal decisions.

Table 2-1. Results of GLMMs (binomial error and logit link function) on the probability of between-year patch fidelity of unsuccessful (sexes combined) prothonotary warblers ($n = 429$) in southern Illinois, 1996 to 2005. Estimates for the random effects* of patch and year are from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Patch reproductive success	$X^2_{1,403} = 27.97$	0.537 \pm 0.102	<0.001
Sex	$X^2_{1,403} = 17.31$	0.942 \pm 0.226	<0.001
Male		0	
Female			
Patch*	$Z = 0.19$	0.017 \pm 0.090	0.424
Year*	$Z = 1.02$	0.203 \pm 0.199	0.115
Removed variables			
Patch conspecific density	$X^2_{1,403} = 2.01$	0.471 \pm 0.332	0.156
Patch area	$X^2_{1,403} = 0.47$	-0.005 \pm 0.007	0.494

^a Estimates are on a logit scale. Estimates of removed variables are from when they were added alone to the final model.

Table 2-2. Results of GLMMs (binomial error and logit link function) on the probability of between-year patch fidelity of unsuccessful male ($n = 220$) prothonotary warblers in southern Illinois, 1996 to 2005. Estimates for the random effects* of patch and year are from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Number of successful neighbors	$X^2_{1,191} = 25.36$	0.642 \pm 0.134	<0.0001
Year*	$Z = 0.56$	0.172 \pm 0.312	0.287
Removed variables			
Patch conspecific density	$X^2_{1,191} = 2.08$	0.583 \pm 0.435	0.181
Age	$X^2_{1,191} = 1.58$	0.437 \pm 0.324	0.211
1 year old		0	-----
2+ years old			
Patch reproductive success	$X^2_{1,191} = 0.25$	-0.069 \pm 0.207	0.715
Patch identity*	-----	0	-----

^a Estimates are on a logit scale. Estimates of removed variables are from when they were added alone to the final model.

Table 2-3. Results of GLMMs (binomial error and logit link function) on the probability of between-year patch fidelity of unsuccessful female ($n = 209$) prothonotary warblers in southern Illinois, 1996 to 2005. Estimates for the random effects* of patch and year are from the final model.

Explanatory variables ^a		Test	Estimate \pm SE	p -value
Final model				
Patch reproductive success		$X^2_{1,181} = 21.92$	0.542 \pm 0.114	<0.001
Age	1 year old	$X^2_{1,181} = 3.41$	-0.739 \pm 0.401	0.067
	2+ years old		0	
Removed variables				
Patch conspecific density		$X^2_{1,181} = 0.20$	0.133 \pm 0.436	0.749
Patch area		$X^2_{1,181} = 0.05$	0.027 \pm 0.187	0.926
Patch*		-----	0	-----
Year*		-----	0	-----

^a Estimates are on a logit scale. Estimates of removed variables are from when they were added alone to the final model.

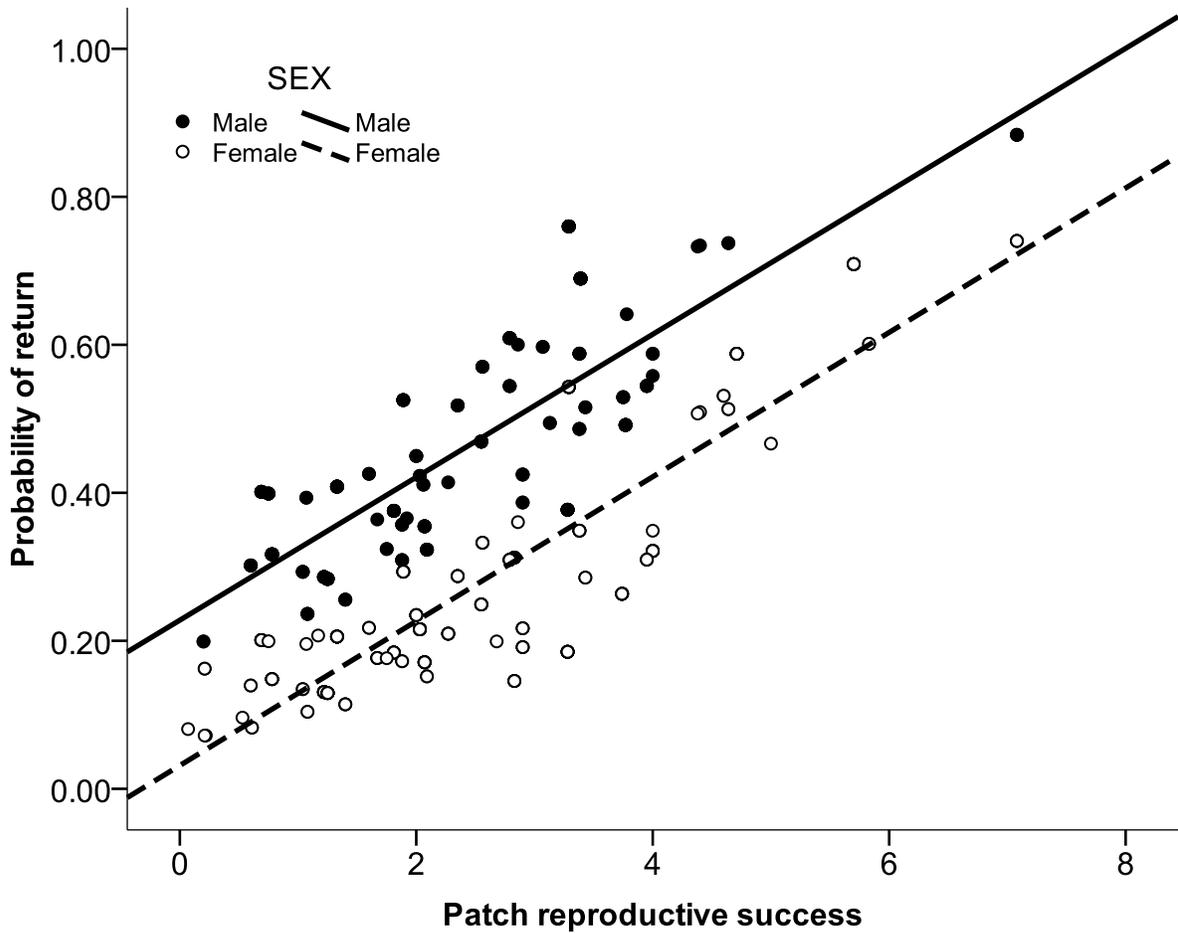


Figure 2-1. Probability that unsuccessful male (closed circles) and female (open circles) prothonotary warblers returned to their patch in relation to increasing patch reproductive success. Points represent return probability for groups of males and females on each patch each year. Values are predicted from the final model and are controlled for the random effects of site identity and year (see Appendix Figure A-1 for actual observed return rates)

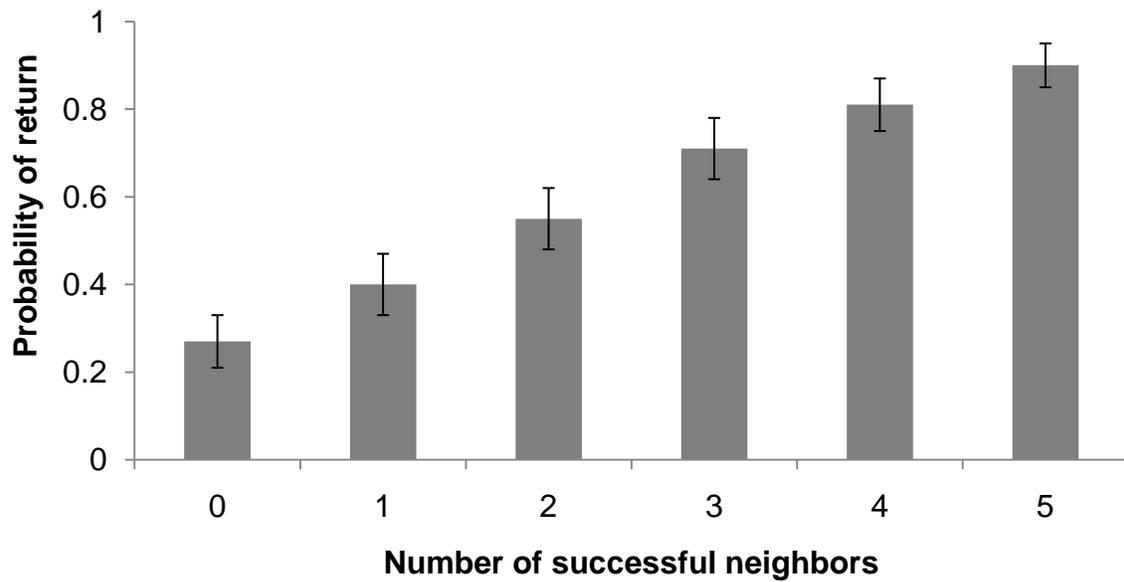


Figure 2-2. Probability that unsuccessful male prothonotary warblers returned to their patch between years in relation to the number of successful conspecific neighbor pairs. Bars represent mean \pm 1 SE values that were predicted from the final model (see Appendix Figure A-2 for actual observed return rates).

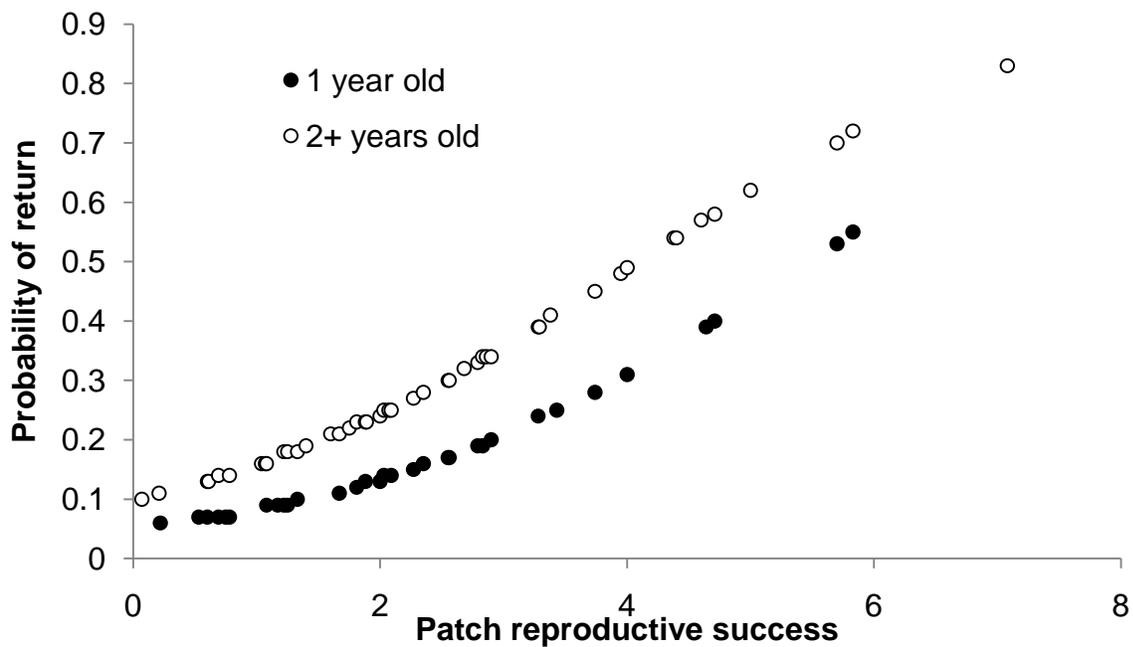


Figure 2-3. Probability that unsuccessful female prothonotary warblers returned to their patch in relation to patch reproductive success and age. Points represent predicted values from the final model (see Appendix Figure A-3 for actual observed return rates).

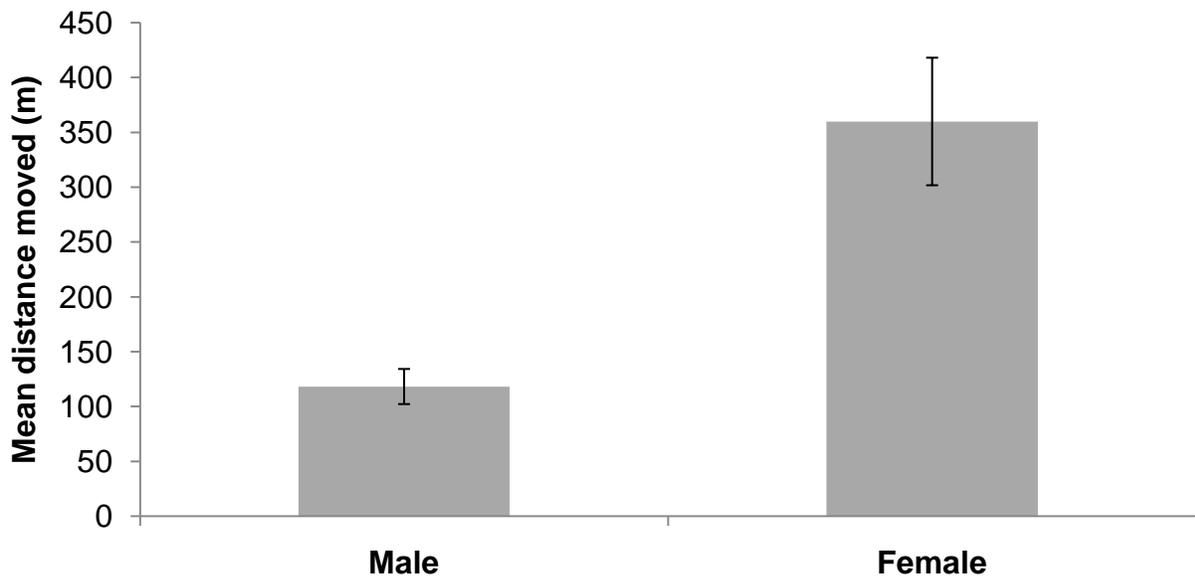


Figure 2-4. Distance moved of all returning birds in relation to sex and PRS. Bars represent mean \pm 1 SE values that were predicted from the final model.

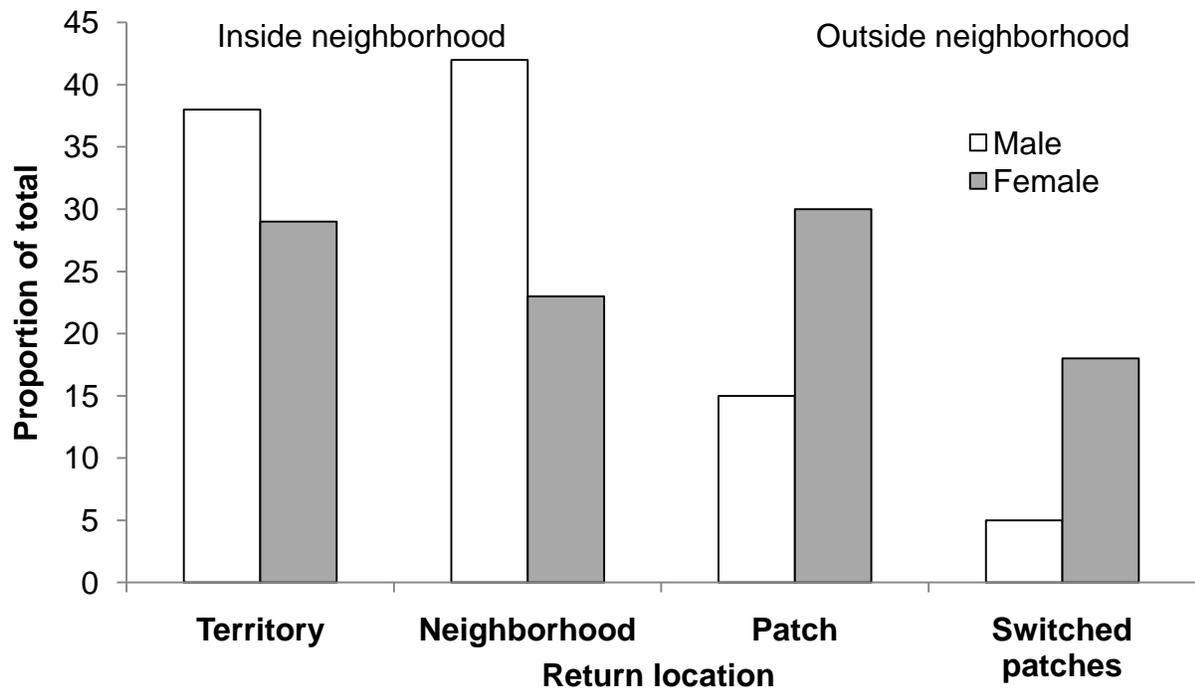


Figure 2-5. Proportion of totals of returning unsuccessful males ($n = 105$) and females ($n = 73$) that returned to locations within and outside of their neighborhood.

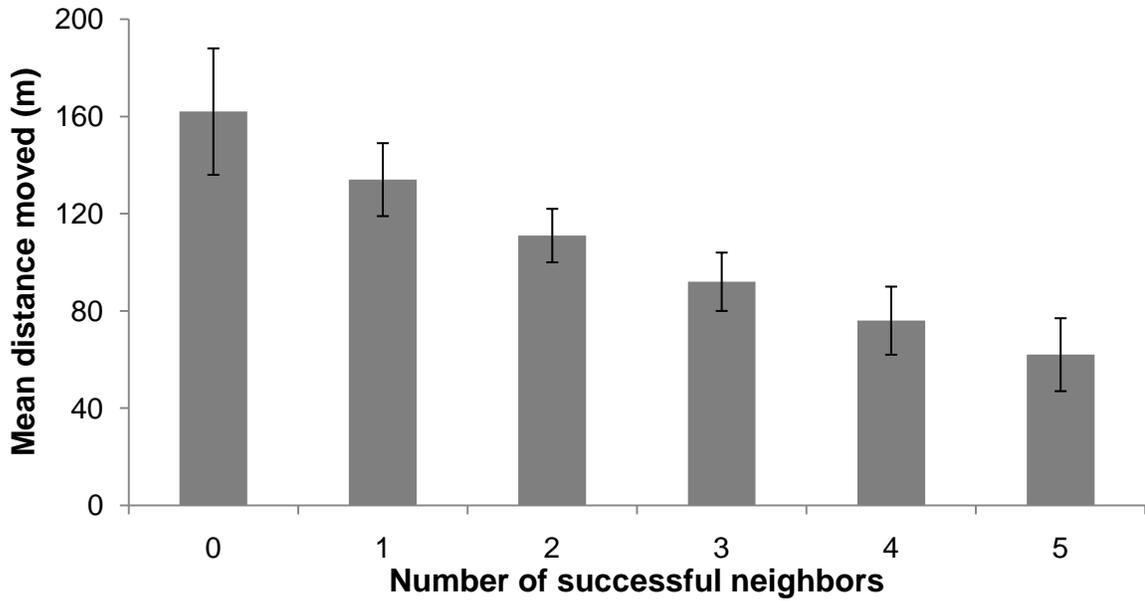


Figure 2-6. Male ($n = 105$) distance moved (m) in relation to neighborhood quality. Bars represent mean ± 1 SE values that were predicted from the final model (see Appendix Figure A-4 for actual mean \pm SE distance moved for males).

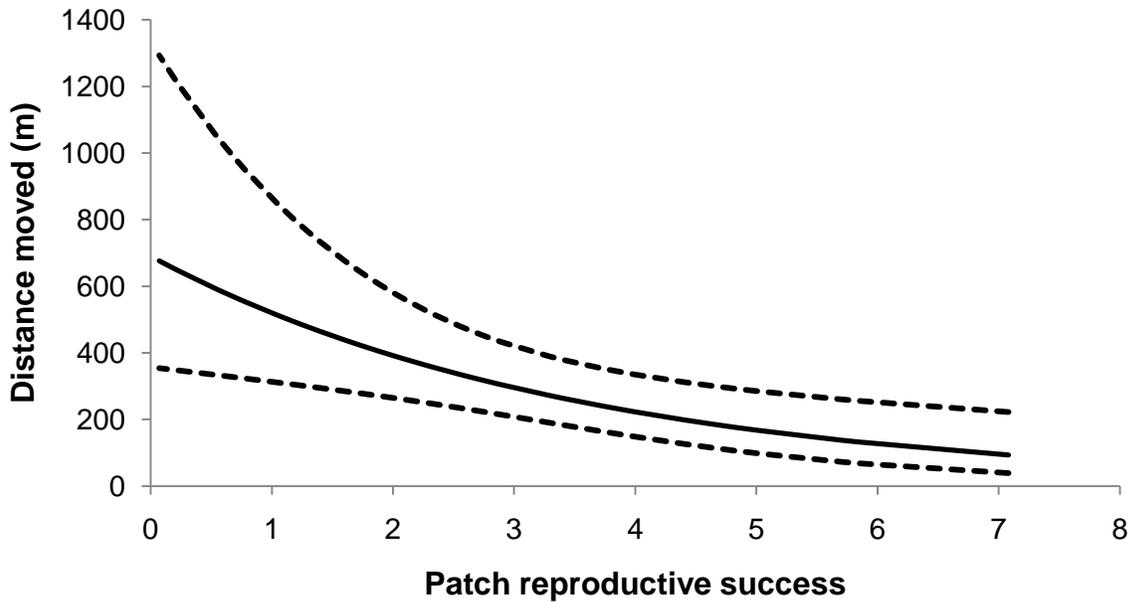


Figure 2-7. Female ($n = 73$) distance moved (m) in relation to patch reproductive success (number of offspring/female/patch/year). Mean (solid line) $\pm 95\%$ C.I. (dashed lines) values predicted from the final model (see Appendix Figure A-5 for actual distance moved for females)

CHAPTER 3
NEIGHBORHOOD FIDELITY OF UNSUCCESSFUL MALES RESULTS FROM BOTH
PUBLIC AND PRIVATE INFORMATION: A ROLE FOR NEIGHBORS AND EXTRA-
PAIR OFFSPRING

Introduction

Long-lived species continually make breeding dispersal decisions throughout their lifetime. These decisions are often condition- or context-dependent because of environmental variation in habitat quality, population dynamics, and intra-specific, and inter-specific interactions (Ims & Hjermann 2001). The sexes also should vary in their dispersal decisions as a result of differences in duties related to typical sex roles during reproduction and the prevailing mating system. Indeed, sex-biased breeding dispersal is widespread in the animal world and in birds is predominately female-biased (Greenwood 1980; Greenwood & Harvey 1982; Clarke et al. 1997). Individuals assess environmental conditions either by their own individual breeding experience (private information) (Switzer 1997; Haas 1998; Hoover 2003b) or by observing the breeding experience of others (public information) (Danchin et al. 2001; Doligez et al. 2002; Doligez et al. 2004). Species that are limited to short tenure on breeding grounds, such as those that are migratory, have limited opportunity to collect public information while breeding and it is thought that this type of habitat assessment is primarily based on information gathered after their own breeding attempt fails (Ottosson et al. 2001; Doligez et al. 2002; Doligez et al. 2004; Betts et al. 2008). Individuals that can accurately assess environmental information can subsequently disperse to better breeding areas and maximize their fitness if the benefits of acquiring information and/or dispersing outweigh the costs (McPeck & Holt 1992).

Private information in the form of individual reproductive success (IRS) is likely the most accurate for predicting future success because it takes into account an individual's own performance that may result from variation in individual quality. High reproductive output typically results in similarly high site and/or territory fidelity for both sexes, whereas failed breeders tend to disperse (Doligez et al. 1999; Hoover 2003b). Assuming some level of predictability in the environment, failed breeders can assess future breeding sites over potentially large spatial scales by observing conspecifics (Boulinier & Danchin 1997). In many species, after juveniles, failed breeders comprise the group that is the most likely to disperse (Switzer 1997; Haas 1998), exhibit sex-biased dispersal (Gavin & Bollinger 1988; Hoover 2003b) and use public information (Danchin et al. 2001).

The role of public information in the dispersal decision-making process of territorial birds has been the subject of intensive recent study. Failed breeders that collect public information must be able to accurately assess their own future reproductive potential based on breeding success of conspecifics. Based on differences in sex roles and mating systems, males and females should assess or interpret their surrounding environment differently (Pärt 1995; Gros et al. 2008). In fact, several studies have found sex differences in prospecting behavior such that males are much more likely to be detected checking the nest contents of conspecifics directly (Ottooson et al. 2001; Doligez et al. 2004). Experimental evidence is mounting for the potential widespread use of public information (Doligez et al. 2002; Betts et al. 2008; Boulinier et al. 2008; Clobert et al. 2009; Redmond et al. 2009); however, the majority of these studies have not explicitly tested for differences between the sexes.

In the majority of avian species, males are more site and territory faithful than females (Clarke et al. 1997). Greenwood (1980) suggested that the mating system could explain the vast majority of dispersal patterns found in birds. In socially monogamous species, which include more than 90% of all avian species (Lack 1968), males defend resources and must compete for territories and mates. Interactions with neighbors, therefore, are an important component of male habitat assessment (Beletsky & Orians 1989; Eason & Hannon 1994; Formica et al. 2004; Sillett et al. 2004). What Greenwood did not know at the time of his seminal paper was the widespread occurrence of extra-pair mating in socially monogamous species (Griffith et al. 2002). Extra-pair (EP) mating opportunity can significantly alter male reproductive success (Albrecht et al. 2007) and could provide strong selection on male dispersal decisions. In many species, the majority of EP matings occur with neighboring females (Yezerinac et al. 1995; Stutchbury 1998; Norris & Stutchbury 2001; Mennill et al. 2002; Formica et al. 2004; Pedersen et al. 2006; Chiver et al. 2008). Therefore, unsuccessful males returning to good sites based on conspecific reproductive success could in fact be using private information based on their own reproductive success via EP matings. Because males can be successful outside of their social pair bond and females cannot (barring the relatively rare occurrence of conspecific brood parasitism), EP mating success and/or opportunity could be the key sex difference influencing breeding dispersal. In fact, local conspecific reproductive success (public information) is likely highly correlated with a male's probability of fledging EP offspring (private information) (Yezerinac et al. 1995; Perreault et al. 1997; Stutchbury 1998; Norris & Stutchbury 2001; Pedersen et al. 2006).

In this study, I investigated whether breeding male prothonotary warblers (*Protonotaria citrea*) responded to private information pertaining to their own reproductive success via EP matings. Prothonotary warblers are socially monogamous with traditional sex roles similar to the vast majority of other avian species (Petit 1999). In addition, their habitat is predictable between years, such that high quality territories and patches in one year tend to be high quality again (Hoover 2003b, 2006). Previous experimental research in this system showed that both male and female prothonotary warblers respond to private information via a “win-stay, lose-switch” decision rule with approximately 80% of double-brooded birds returning to their patch whereas unsuccessful individuals were the most dispersive (Hoover 2003b). Furthermore, failed breeders were the only group to show a significant sex-bias with females being more dispersive than males. Further studies revealed that unsuccessful males and females, experimentally exposed to and tested at varying levels of conspecific reproductive success, responded to public information at different scales (Chapter 2). Unsuccessful females were more likely to return to their patch based on overall patch reproductive success (# offspring/female/patch/year) whereas unsuccessful males made this decision based on the number of successful neighbors. In fact, males were more likely to return to their neighborhood than females between years suggesting that the sexes, exposed to similar public information, seem to interpret habitat quality differently (Chapter 2).

Here I experimentally examined the effect of public (neighborhood conspecific reproductive success) and private information (EP mating success) on neighborhood fidelity of male prothonotary warblers unsuccessful in their own nests. I focused on the

between-year movements of individually marked warblers in relation to the number of successful neighbors and the siring of EP offspring. Specifically, I experimentally induced reproductive failure of focal pairs and improved neighborhood quality by manipulating neighbor reproductive success in an attempt to fledge EP offspring of focal males. I predicted that the majority of EP offspring would be sired with neighbors and, therefore, expected that the probability of a male fledging EP offspring would increase with an increase in the number of successful neighbors. I predicted that focal males that were unsuccessful in their own nesting attempts would rely on their own private information pertaining to the fledging of their EP offspring with a neighboring female such that their neighborhood fidelity would be higher than focal males without EP mating success.

Materials and Methods

Study Area and Study Organism

I conducted this research within the Cache River Watershed in Illinois, USA (37° 18' N, 88° 58' W). I chose 12 study sites of which four were experimental and eight were not manipulated. For more details regarding study location and habitat characteristics see Chapter 2. Non-manipulated sites are those sites with nest boxes that are monitored in the same fashion as experimental sites except that nest boxes are not moved onto poles during the study, and predation is not experimentally controlled. Therefore, non-manipulated sites serve as a control and the responses of the birds are similar to what would be expected from naturally occurring populations with non-experimental modes of nest predation. Each study site had at least eight breeding pairs of warblers each year.

The prothonotary warbler is a migratory songbird that breeds in the central and eastern United States and winters in areas of Central and South (Petit 1999). This species nests in secondary cavities, prefers to nest over standing water in bottomland forests and swamp. The prothonotary is territorial and socially monogamous (Petit & Petit 1996) and readily uses nest boxes when available (Petit 1989; Blem & Blem 1994; Hoover 2003b). Additional details of its natural history are given elsewhere (Petit 1999; Hoover 2003a, 2006).

Prothonotary warblers are ideally suited for testing the neighborhood hypothesis as it relates to extra-pair mating success and between-year fidelity to neighborhoods (neighborhood fidelity hereafter) because: (1) they are restricted to a particular habitat type, which simplifies the process of relocating neighborhood faithful and dispersed birds; (2) their habitat occurs in discrete patches which makes capturing the majority of likely sires possible; (3) they use nest boxes, allowing me to experimentally manipulate the nesting success of individual pairs of birds; (4) by excluding predation I can guarantee that any offspring fledged will be genetically sampled; and (5) it was previously demonstrated experimentally that neighborhood fidelity of unsuccessful males is based on public information and increases with an increase in the number of successful neighbors (0 to 5) (Chapter 2). Here I study factors associated with variation in the neighborhood fidelity of unsuccessful males as it pertains to public information and/or EP mating success.

Monitoring Individuals and Manipulating Nesting Success

During 2000 to 2004 I monitored and experimentally manipulated breeding populations of prothonotary warblers using nest boxes that were attached to trees and placed on study sites in a grid formation (see details in Chapter 2). I captured or

re-sighted all individual warblers on all study sites every year. For detailed capture and marking techniques, see Chapter 2. I collected ~10- μ l blood samples by brachial puncture using a 26G1/2 (BD-Becton-Dickinson) needle and micro-hematocrit tubes (Fisher Scientific, Pittsburgh, PA, USA). I stored all blood samples in Queen's lysis buffer (Seutin et al. 1991) at room temperature while in the field and later stored all blood samples at -20°C. On experimental study sites I knew the identity of the male and female associated with every nesting attempt each year. Adults were aged as either second-year (SY; i.e., 1 year old) or after second-year (ASY; 2+ years) based on plumage (Pyle 2001) and morphometric characteristics of known-age birds (unpublished data J. Hoover).

During each year from 2002 to 2004 I experimentally manipulated the nesting success of individual pairs on each of the four experimental study sites (area range, 10 to 44 ha) so that approximately 33% of pairs each year were randomly assigned to a focal "failure" group and failed to fledge offspring from their own nest. The remaining neighbor pairs successfully reproduced on each site (similar to natural levels of reproductive output; Hoover 2001). My intent was to surround unsuccessful focal males with all successful neighbors in an attempt to maximize reproductive success of focal males via extra-pair paternity. Previous research (Chapter 2) showed that return rates of males increased with the number of successful neighbors, regardless of how many neighbors a male had (neighborhood density). Neighbors were defined as warbler pairs with territories adjacent to the focal pair and limited to a radius of three nest-boxes (~160 m) in all directions, which constituted approximately one territory deep beyond the focal pair.

On experimental sites, I removed nest boxes from trees and reattached them to two pieces of 1.50-cm-diameter greased conduit placed in the ground and standing one meter away from the original nest tree. Nest boxes placed on conduit were safe from nest predation, allowing me to control when predation occurred and making certain that I could take blood samples from all of the nestlings. I then manipulated all nesting attempts of focal pairs (failure treatment) to simulate nest predation and prevent them from fledging any nestlings. For more detailed information about simulated nest predation see Chapter 2. I relocated these nestlings to the nests of foster parents on other sites not included in the experiment.

I monitored all nesting activity of every pair on every study site (see Hoover 2003a, 2006) for detailed monitoring protocol] and recorded the number of warbler offspring produced by each pair for each nesting attempt. At the end of each breeding season I had complete information on the identity and reproductive output (warbler offspring fledged) of all warblers including focal pairs and neighbor prothonotary warblers breeding on my study sites. Individuals that were assigned to the failure treatment group in one year were never re-sampled in a subsequent year. Therefore, my sample sizes for focal males represent the total number of males that were unsuccessful and their extra-pair mating success and neighborhood fidelity in the year after assignment to the failure treatment.

Documenting Site Fidelity and Local Breeding Dispersal

I determined the identity of every color-marked individual and captured and color-marked any individuals that were not banded so that all individuals were individually marked every year. For the purposes of this paper, I focused on the returns of those males that failed to fledge any offspring from their own nest in the previous year. I

determined whether or not unsuccessful individuals returned to their neighborhoods the following year and searched for any dispersing color-marked birds within a 500-m wide area surrounding each study site. During the years of my study, breeding density on patches did not reach saturation (population densities increased every year) and were unlikely to affect an individual's ability to return to the patch (W. Schelsky, unpublished data).

In 2000 to 2001 I examined ambient levels of neighborhood fidelity for unsuccessful males on both experimental and non-manipulated sites for a comparison prior to my experimental manipulation. I continued monitoring non-manipulated sites during 2002 to 2004 with ambient levels of nest predation to compare to my experimental sites to show the effect of my manipulated neighborhoods on the neighborhood fidelity of unsuccessful males. I also genetically sampled complete families ($n = 41$) on non-manipulated sites in 2002 to show that my treatments did not directly affect rates of extra-pair paternity. Because of high rates of nest predation I was unable to sample entire neighborhoods on non-manipulated sites.

Paternity Analyses

DNA was extracted from all blood samples using Qiagen® DNeasy tissue kits (Qiagen Inc., Valencia, CA, USA). I identified eight microsatellite loci by screening published primer sequences from other wood warbler species (Parulidae) (Table 3-1) (Dawson et al. 1997; Winker et al. 1999; Stenzler et al. 2004). I searched for cross-amplification of each locus for prothonotary warblers first on a temperature gradient. Once I identified an optimal annealing temperature I checked for allelic polymorphisms for each locus. Forward primers were labeled with either FAM or HEX (Eurofins MWG operon, Huntsville, AL, USA) 5'-fluorescent labels for genotyping. PCR reactions were

performed in 12-tube strips using a PCR Express® thermal cycler (Thermo Scientific, Waltham, MA, USA). The cycling profile was 1 cycle at 94°C for 3 min, 35 cycles of 30 s at 94°C, 60 s at the locus-specific annealing temperature, and 60 s at 72°C followed by a final extension cycle of 5 min at 72°C. Thermal cycling profiles were similar for all loci except for the annealing temperature (Dpu01 at 58°C, Dpu03 at 59°C, Dpu16 at 58°C, Lsw12 at 54°C, Vecr04 at 60°C, Vecr05 at 61°C, Vecr06 at 56°C, and Vecr07 at 63°C). Each 12.5- μ l reaction contained at least 50 ng genomic DNA, 0.24 μ M of each primer, 800 μ M dNTPs, 1x PCR buffer, 0.5 U of *Taq* polymerase (Eppendorf, Hauppauge, NY, USA), and a primer-specific MgCl₂ concentration (0.5 to 1.5 mM). Fragment sizes for all PCR products were analyzed by the University of Florida Biotechnology Core Lab using an ABI 3730 (Applied Biosystems Inc., Foster City, CA, USA). Fragment data were sized using GENESCAN 3.7 and scored using GENOTYPER software (Applied Biosystems Inc.).

Each set of primers was tested on a set of adult prothonotary warblers ($n = 249$) breeding in 2002 to assess allelic diversity, test for Hardy-Weinberg equilibrium, the frequency of null alleles (CERVUS, Marshall et al. 1998), and linkage disequilibrium (GENEPOP 2007, Rousset 2008) (Table 3-1). All individuals ($n = 2425$) were genotyped at more than four loci and the majority (> 99%) were genotyped at six loci or more. Allelic diversity ranged from 6 to 26 alleles 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 0.001 to 0.063, which is considered rare, and should not cause sufficient concern over exclusion probability for paternity analyses (Dakin & Avise 2004). I calculated the genotyping error based on a re-run sub-sample of

3.97% ($n = 2424$) of all individuals at all loci that showed an overall error rate of 0.4%.

The overall amplification success for this sub-sample was 99.98 ± 0.016 % (mean \pm SD) of all alleles.

Parentage analyses were initially completed using CERVUS 3.0 (Marshall et al. 1998). Males were excluded as putative fathers by analyzing broods with both known mother and putative father. Single-sex parentage (paternity) was assigned at a 95% (strict) confidence level for each offspring both with ($n = 1607$) and without ($n = 15$) a known genotyped mother. For my initial exclusion of putative males I ran simulation parameters set for CERVUS as follows. Number of candidate fathers: six, which is the same as the maximum number of offspring per brood. Proportion of males sampled: I assumed 90% given that all of the breeding males on the sites were sampled, but allowing for floater males that went undetected. Proportion of loci typed: this was assumed to be 95%. Proportion of loci mistyped: I rounded up to 1% for the purpose of the simulation. Males were excluded as the true father based on LOD scores which are derived from the collective likelihood ratios across loci (Marshall et al. 1998; Kalinowski et al. 2007).

Offspring identified as extra-pair ($n = 116$) on experimental sites, based on exclusion of putative father, were then re-grouped according to site by year and re-run using the putative mother and a candidate pool of males present on the site in that year. This was the most conservative approach to identifying sires because I limited the candidate pool to only those males known to be present. If I was unable to identify sires using only males detected in that year, I reanalyzed offspring using all candidate males from the study population in the event that a given male was not detected on a site in a

given year. Offspring assigned to a particular male not detected in that year were only done so in the event that the male was seen on that site or the nearest site at some point during the study. In two cases a male was identified as a sire, but could not have feasibly done so based on where they had been detected in that year (i.e., breeding on a site more than 3 km away). In total, on experimental sites, I identified the sire for 99.4% ($n = 1462$) of all offspring, including within- and extra-pair, on experimental sites. I was able to identify the sire for 92.2% ($n = 116$) of all EP offspring.

Statistical Analyses

To determine whether the experimental manipulations directly influenced the return of unsuccessful males to their neighborhood I used stepwise (forward-stepping) multiple logistic regression analyses (SPSS 2007) to determine whether time period (pre- vs. post-manipulation), site status (experimental vs. non-manipulated) or the interaction explained the neighborhood fidelity of individual males that were unsuccessful in the previous year. I used a p -to-enter value of 0.05. Neighborhood fidelity was the binary dependent variable (i.e., birds returned or did not return to their neighborhood where they had been unsuccessful). Time period and site status were binary independent variables. I also tested whether experimental site status during the years of the manipulations increased the average number of successful neighbors using a t-test with unequal variance.

On experimental sites I calculated rates of EP matings for offspring, broods and males for all individuals, including focal pairs and neighbors, for each year separately and averaged them across years (2002 to 2004). I compared the rate of extra-pair offspring on experimental and non-manipulated sites in 2002 only using a chi-square test. I compared the number of EP offspring sired, EP reproductive success (yes or no),

number of actual neighbors (0 to 7), and age (SY, 1 year old; or ASY, 2+ years old) of focal and neighbor males to determine whether my random selection of focal males resulted in a representative sample of the population. For each I used a generalized linear mixed model (GLMM) using GLIMMIX procedures in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) to determine whether each of the dependent variables listed above were related to their experimental status (failure vs. success). I used a Poisson distribution with a log-link function for the number of EP offspring sired and the number of actual neighbors, and a binomial distribution with a logit-link function for both EP mating success (yes or no) and age. The Poisson distribution works best when the response variables are count data (SAS Institute Inc. 2008). For all Poisson GLMMs I used the Kenward-Roger adjustment for calculating the degrees of freedom (Kenward & Roger 1997). The Kenward-Roger adjustment is more robust than SAS default methods for small sample sizes and uneven block designs (Kenward & Roger 1997; Kowalchuk et al. 2004). Because the penalized quasilikelihood (PQL) method, the default in SAS, can be biased for binary data I used the Laplace approximation method for approximating the likelihood for all GLMMs using a binomial distribution (Bolker et al. 2009). Because I had many individuals return to my study sites between years, for comparisons between the “successful” and “failed” group I used a repeated measures design by adding a random effect of year for individual males. I also blocked my analyses by study site to account for non-independence.

To examine which factor best explained neighborhood fidelity of focal males ($n = 91$) I used a generalized linear mixed model (GLMM) using GLIMMIX procedures in SAS 9.2 with a binomial error distribution (response variable coded as “0” and “1”) and a

logit-link function to model the probability a focal male returned to their neighborhood. I included number of successful neighbors (0 to 5) and success via extra-pair (yes or no) as fixed effects. I also included patch identity and year as random effects to control for non-independence of observations. I evaluated the importance of fixed effects using Wald-type statistics reported by the GLIMMIX procedure in SAS. Beginning with a full model that included all fixed effects I used a backward stepwise approach by progressively eliminating non-significant variables ($\alpha = 0.05$).

To examine whether males with EP young were of better quality than those without EP young I compared condition (standardized residuals from mass x tarsus regression) and mass for focal males with and without EP offspring. I also compared age for males with and without EP offspring using a chi-square test, because age has been shown to influence both adult breeding dispersal (Winkler et al. 2004; Eeva et al. 2008) and rates of extra-pair in other species (Bouwman et al. 2007; Schmoll et al. 2007; Lehtonen et al. 2009). All values are reported as means \pm 1 SE unless otherwise indicated.

Results

Experimental vs. Non-Manipulated Sites

A total of 91 and 78 males were unsuccessful on experimental and non-manipulated sites, respectively, during 2002 through 2004. Return rates of unsuccessful males did not differ for experimental and non-manipulated sites in the two years prior to my experiment, and, by manipulating neighborhood success on experimental sites, unsuccessful focal males returned at a significantly higher rate to the neighborhood than those on non-manipulated sites (Figure 3-1; logistic regression: interaction pre/post-manipulation and experimental/non-manipulated site $X^2_1 = 14.49$,

$n = 224$, $p < 0.001$). During the experimental years, males on experimental sites had more successful neighbors (2.27 ± 0.137) than those on non-manipulated sites (0.35 ± 0.068) [two-tailed t-test (unequal variances); $t_{167} = -11.98$, $p < 0.001$].

Frequency of Extra-Pair Nestlings

Of all pairs (successful and unsuccessful) on experimental sites from 2002 to 2004, $7.4 \pm 2.4\%$ (mean \pm SD) of all nestlings ($n = 1462$) were extra-pair (EP). I found no evidence of conspecific brood parasitism because all nestlings ($n = 1462$) were assigned to the putative mother. The average proportion of broods and males with at least one EP offspring across years was $20.5 \pm 5.0\%$ (mean \pm SD) ($n = 409$) and $18.8 \pm 3.0\%$ (mean \pm SD) ($n = 306$), respectively. The rate of EP offspring in 2002, the first year of the study, did not differ between non-manipulated (5.6% , $n = 160$) and experimental (5.7%) ($n = 349$) sites ($X^2_1 = 0.004$, $p = 0.949$) demonstrating that my manipulation did not directly affect rates of EP nestlings.

Unsuccessful Focal vs. Neighbor Males

Forty-seven percent ($n = 91$) of unsuccessful focal males and 84% of their successful male neighbors ($n = 130$) returned to their neighborhood in the subsequent year (chi-square: $X^2_1 = 27.18$, $p < 0.001$) which demonstrates that, in general, unsuccessful males are more dispersive. As an indication that focal males represented the population at large, I found no difference in the total number of EP offspring sired (GLMM, $\beta \pm SE = -0.054 \pm 0.234$, $X^2_{1, 335} = 0.05$, $p = 0.818$), the probability of siring at least one EP offspring (GLMM, $\beta \pm SE = -0.03 \pm 0.29$, $X^2_{1, 92} = 0.01$, $p = 0.911$), total number of neighbors (GLMM, $\beta \pm SE = -0.085 \pm 0.070$, $X^2_{1, 312} = 1.48$, $p = 0.224$), or age (GLMM, $\beta \pm SE = -0.388 \pm 0.246$, $X^2_{1, 97} = 2.50$, $p = 0.114$) for focal versus neighbor males.

Unsuccessful Focal Males

I intended to make all neighbors of focal males successful, but in a few cases randomly-chosen focal males were neighbors of other focal males. The number of actual neighbors, however, was highly correlated with the number of successful neighbors (regression: $R^2 = 0.787$, $F_{1, 89} = 329.54$, $p < 0.001$). Of the 91 focal males, 13% sired at least one extra-pair offspring. Of those males, 93% ($n = 12$) had their EP offspring fledge and 91% of males that fledged extra-pair offspring ($n = 11$) did so with a neighbor. The average distance from the nest of a focal male to his fledged extra-pair offspring was 114.4 ± 28.4 m (mean \pm SD) ($n = 11$) (Range 76.7 to 167.0 m). The probability of gaining at least one EP fertilization was positively correlated with the number of actual neighbors (i.e., neighborhood density) (Pearson's correlation: $r = 0.209$, $df = 7$, $p = 0.038$) and fledging at least one EP offspring was positively correlated with the number of successful neighbors (Figure 3-2; Pearson's correlation: $r = 0.284$, $df = 5$, $p = 0.006$).

Ninety-one percent ($n = 11$) of focal males that fledged EP offspring returned to their neighborhoods compared with only 41% ($n = 80$) of those without EP success (Figure 3; chi-square: $X^2_1 = 9.57$, $p = 0.002$). I examined neighborhood fidelity of focal males using GLMM (binomial distribution, logit-link) to determine whether public information and/or EP mating success best explained focal male return rates to the neighborhood. Unsuccessful males were more likely to return to their neighborhood if they fledged at least one EP offspring (GLMM, $\beta \pm SE = 2.23 \pm 1.09$, $X^2_{1, 81} = 4.16$, $p = 0.041$) regardless of the number of successful neighbors (Figure 3-4). Only those focal males without EP mating success showed an increase in their return rate to the neighborhood with an increase in the number of successful neighbors (Figure 3-4;

GLMM, $\beta \pm SE = 0.617 \pm 0.209$, $X^2_{1, 81} = 8.69$, $p = 0.003$). Unsuccessful females ($n = 92$) that were experimentally assigned to the “failure” treatment group were less likely than the unsuccessful males (28% vs. 47%) to return to their neighborhoods (chi-square: $X^2_1 = 7.025$, $p = 0.008$).

Because the number of actual and successful neighbors was correlated and male-male competition may lead to non-random sorting of males I wanted to make sure that higher return rates of males in better neighborhoods was not an artifact of male quality. I found that male condition (i.e., quality) was actually negatively associated with the number of successful neighbors (Pearson’s correlation: $r = -0.364$, $df = 65$, $p = 0.002$) which contradicts the idea that better quality males are in bigger, better neighborhoods. Among focal males, condition (two-tailed t-test: $t_{67} = -0.605$, $p = 0.547$) and mass (two-tailed t-test: $t_{67} = -0.600$, $p = 0.551$) did not differ between males that did and did not fledge EP offspring. Older (i.e., ASY) males made up a larger percentage of those focal males with EP offspring (73%; $n = 11$) than those without EP offspring (40%; $n = 80$) (chi-square: $X^2_1 = 4.20$, $p = 0.040$). Unsuccessful males that returned to their neighborhood after fledging EP offspring tended to be more successful at gaining EP fertilizations in the next year than those that responded to the number of successful neighbors [63% ($n = 8$) EP males vs. 30% ($n = 37$) non-EP males; chi-square: $X^2_1 = 3.083$, $p = 0.079$].

Discussion

I found compelling experimental evidence in a migratory songbird that breeding dispersal decisions of males unsuccessful in their own breeding attempts are based on both private and public information. For male prothonotary warblers, unsuccessful individuals were more likely to disperse from their neighborhood in the subsequent

season than their successful conspecifics, demonstrating that, indeed, unsuccessful males are more dispersive. However, unsuccessful males, a group expected to use public information (Chapter 2), did show enhanced neighborhood fidelity if they fledged offspring from a neighbor's nest via extra-pair (EP) mating, demonstrating that private information influenced the dispersal of some "unsuccessful" individuals. In fact, 91% of unsuccessful males successful via EP mating ($n = 11$) returned to their neighborhood, which is similar to the 84% return rate for those neighbors that had been successful in their own breeding attempts (chi-square: $X^2_1 = 0.694$, $p = 0.405$). Additionally, the probability that an unsuccessful male fledged at least one EP offspring increased with an increase in the number of successful neighbors and more than 90% of those EP matings occurred with female neighbors. It appeared that only if a male was unsuccessful on all fronts (failure of own nest and no EP offspring in neighbor's nest), did they positively respond to public information in the form of number of successful neighbors. This is the first study, to my knowledge, that has demonstrated the use of private information, in the form of reproductive success via fledging of EP offspring, in dispersal decisions of unsuccessful breeding males.

No other study of territorial birds has simultaneously examined how conspecific reproductive success and EP mating success compete to influence breeding dispersal decisions. Howlett & Stutchbury (2003), however, examined whether EP fertilizations influenced site fidelity of male and female hooded warblers (*Wilsonia citrina*). In their study, females tended to return to the study site if they had cuckolded their mate, but there was no such pattern involving EP matings and returns for males. The distinction between my study and theirs was that my males actually fledged EP offspring and their

test was of EP fertilizations only (Howlett & Stutchbury 2003). So actual success via EP mating, or the fledging of EP offspring may be required to elicit returns of those males, but further controlled studies are required to determine specifically what information EP males used in their dispersal decisions.

It is possible that males have the ability to determine if their EP offspring fledge given that they appear to monitor neighbor success (Chapter 2). The few studies that have examined the behavior of prospectors collecting information from conspecifics have shown a definite sex-bias such that males are observed more often than females monitoring the nest contents or nest attendance of conspecifics (Ottosson et al. 2001; Pärt & Doligez 2003; Doligez et al. 2004; Dittmann et al. 2007). In an experimental test of prospecting, Pärt & Doligez (2003) increased brood size to examine whether parental feeding activity increased visitation to those nests by prospectors and whether those visits subsequently resulted in nearby settlement the next year. They found that the majority of individuals seen at nests were males and those that later settled where they had prospected were almost entirely males that had been known to fail in their own breeding attempt. The authors did not know or test whether EP paternity influenced male prospecting and/or dispersal behavior; therefore, males that were prospecting could have been collecting private information on the presence or quality of their own EP offspring.

Success via extra-pair mating may be a previously unexplored explanation for the sex-bias in breeding dispersal in my system and other socially monogamous bird species. The proportions of males, broods, and offspring that had, contained, or were extra-pair in my study were similar to other species of territorial, socially monogamous

songbirds (Griffith et al. 2002). Successful breeders of both sexes, in general, show similar high rates of site fidelity and generally do not contribute to the observed sex-bias in breeding dispersal (Gavin & Bollinger 1988; Payne & Payne 1993; Haas 1998; Doligez et al. 1999; Hoover 2003b; Citta & Lindberg 2007). Reproductive failure in one year, however, causes individuals to be more dispersive in the next. In my experiment, “unsuccessful” males were less dispersive than unsuccessful females supporting the conclusion that unsuccessful individuals show the expected sex-biased breeding dispersal pattern that has been documented in the majority of avian species (Greenwood & Harvey 1982; Clarke et al. 1997).

Unsuccessful breeders returning to a highly successful neighborhood may be forced to retain their formerly bad territory due to high between-year predictability of habitat quality and the high return rates of neighbors (Hoover 2003a). For females, this scenario could equal complete reproductive failure in consecutive breeding seasons, whereas males may still be successful via EP mating. Under this scenario females could escape this fate only if conspecific brood parasitism was common, but I found no evidence of conspecific brood parasitism in my system. Only if females could more reliably trade-up to a successful territory in their former neighborhood should they respond to neighbor success in a way similar to males. Females were not, however, more likely than males to trade-up if they returned to the neighborhood [46% females ($n = 26$), 46% males ($n = 43$); chi-square: $X^2_1 = 0.01$, $p = 0.977$], making dispersal out of the neighborhood possibly the best way for unsuccessful females to improve their breeding success in the subsequent year.

Extra-pair mating success could explain sex-biased breeding dispersal if male EP mating success in one year was a good predictor of their EP mating success in the next. Sixty-three percent of “unsuccessful” males that returned to their neighborhood between-years after fledging EP offspring gained EP fertilizations again versus only 30% of those that responded to the number of successful neighbors. This suggests that a decision rule where males return to locations where they experienced success via EP matings may be adaptive and may select for reduced dispersal in males, but not females. Although I do not know why females chose the EP mates that they did (Chapter 4), such as “good genes” or “compatible genes” (see Akçay & Roughgarden 2007 for a review of the competing hypotheses), it may be that males simply return to areas where they are likely to encounter the same female/s that preferred them in the past, given that successful neighbors likely returned to their territories at ~80% (Hoover 2003a).

The main benefit of using public information is to locate habitat of relatively high quality compared to what an individual has already experienced (Boulinier & Danchin 1997). What cannot be gleaned from public information, and can only truly be assessed from private information, is how well an individual will perform or compete in a particular habitat. Competition, food availability, parasites, and mating opportunity can differentially affect individuals in ways that are not necessarily predicted by public information; hence, dispersal decisions should be context- or condition-dependent (i.e., quality, mate compatibility, experience, etc.) (Ims & Hjermann 2001). Therefore, it is not surprising that EP mating success influences male neighborhood fidelity and only those males that lack information regarding where they themselves can be successful should

rely on public information. I acknowledge that public information is very important for first-time breeders and long-distance dispersers that typically have no previous breeding experience in a particular area (Danchin et al. 2001).

The use of public information in habitat selection could lead to a density-dependent deterioration of habitat quality simply because many individuals using the same information may settle there to breed. Indeed, in some situations the persuasion of socially acquired information can potentially lead to “informational cascades” (Giraldeau et al. 2002; Rieucou & Giraldeau 2009) where the use of public information can either result in no net gain or even be costly. Breeders among higher densities of conspecifics may suffer from reduced reproductive success simply through the negative effects of density-dependence (Doligez et al. 2003; Rodenhouse et al. 2003; Sillett et al. 2004) or benefit from Allee effects, or increased fitness directly attributable to conspecific density. Therefore, public information should only lead to conspecific attraction if the cost of reduced habitat quality via density-dependence is outweighed by benefits of Allee effects (Donahue 2006). In my study, and many others, males mating among a higher density of conspecifics show a higher rate of EP fertilizations (Yezerinac et al. 1995; Westneat & Sherman 1997; Norris & Stutchbury 2001). The neighborhood fidelity of unsuccessful males in response to both their EP mating success and neighbor success could be due to Allee effects on mating success. Indeed, the idea of territorial males of socially monogamous species clustering in the form of “hidden leks” in direct response to female pursuit of extra-pair copulations has been proposed to explain Allee effects of conspecific density (Wagner 1998).

Greenwood (1980) proposed that the mating system in most mammals and birds can explain sex-biased breeding and natal dispersal patterns seen in nature. In most socially monogamous birds sex-biased dispersal is female biased, and Greenwood assumed that males have more to lose if they disperse, because being familiar with the territory would benefit males more than females. Although familiarity with a territory or neighbors has been shown to enhance a male's ability or willingness to defend their territory (Stamps 1987; Pärt 1994, 1995; Takeuchi & Honda 2009) and lowers the costs associated with defending it (Stamps 1987; Eason & Hannon 1994; Temeles 1994; Schwartz et al. 2007), very few have shown a direct, male-specific fitness benefit of nesting in a familiar area [but see (Beletsky & Orians 1989; Piper et al. 2008)]. Additionally, in my study, unsuccessful males retaining their bad territory are unlikely to reap the benefits of territory familiarity because nest predation is the major factor influencing nesting success (Hoover 2006), which likely overrides any subtle benefits associated with territory defense

Conclusions

What Greenwood did not know at the time was that EP mating is widespread among socially monogamous species (Griffith et al. 2002) and even moderate to low rates of EP matings can provide enough opportunity for sexual selection (Albrecht et al. 2007). Several studies, including this one, have found that older males are more likely to sire EP offspring (Weatherhead & Boag 1995; Kempenaers et al. 1997; Perreault et al. 1997; Bouwman et al. 2006; Kleven et al. 2006; Schmoll et al. 2007), which in the past has been both explained by either increased experience or good genes. What has not been tested, to the best of my knowledge, is whether older males, because of their familiarity with a territory, neighborhood, and/or site, may increase their fitness by

continually returning to or dispersing to areas with known EP mating opportunities. Carefully controlled experiments, in long-lived species, are needed to determine whether dispersal decisions linked to the fledging of EP offspring are widespread among socially monogamous, territorial species. In addition, cases where age influences male EP mating success should be closely examined for the correlated effects of site and/or territory familiarity on EP paternity. It may be that Greenwood, without knowing why, was right all along, and territory and/or site familiarity does pay for males, in the quest for EP matings.

Table 3-1. Summary statistics of eight microsatellite loci used to determine paternity in prothonotary warblers; n , number of individuals genotyped; N_A , number of alleles; H_O , observed heterozygosity; H_E , expected heterozygosity, P_{MEX} , probability of maternal exclusion (overall = 0.997), P_{PEX} , probability of paternal exclusion with known mother (overall = 0.999).

Locus	n	N_A	Allele size range	H_O	H_E	P_{MEX}	P_{PEX}	Estimated frequency of null alleles
Dpu 01 ^a	249	24	138-184	0.900	0.888	0.643	0.782	0.0077
Dpu 03 ^a	249	6	124-144	0.542	0.569	0.164	0.292	0.0254
Dpu 16 ^a	249	16	150-180	0.908	0.913	0.697	0.822	0.0017
Lsw 12 ^b	249	26	403-461	0.888	0.925	0.737	0.848	0.0201
VeCr 04 ^c	249	12	120-159	0.582	0.583	0.204	0.386	0.0191
VeCr 05 ^c	249	6	200-212	0.635	0.609	0.199	0.354	0.0149
VeCr 06 ^c	249	9	307-331	0.755	0.713	0.317	0.498	0.0341
VeCr 07 ^c	249	20	111-153	0.803	0.914	0.699	0.823	0.0635

^a(Dawson et al. 1997), ^b(Winker et al. 1999), ^c(Stenzler et al. 2004)

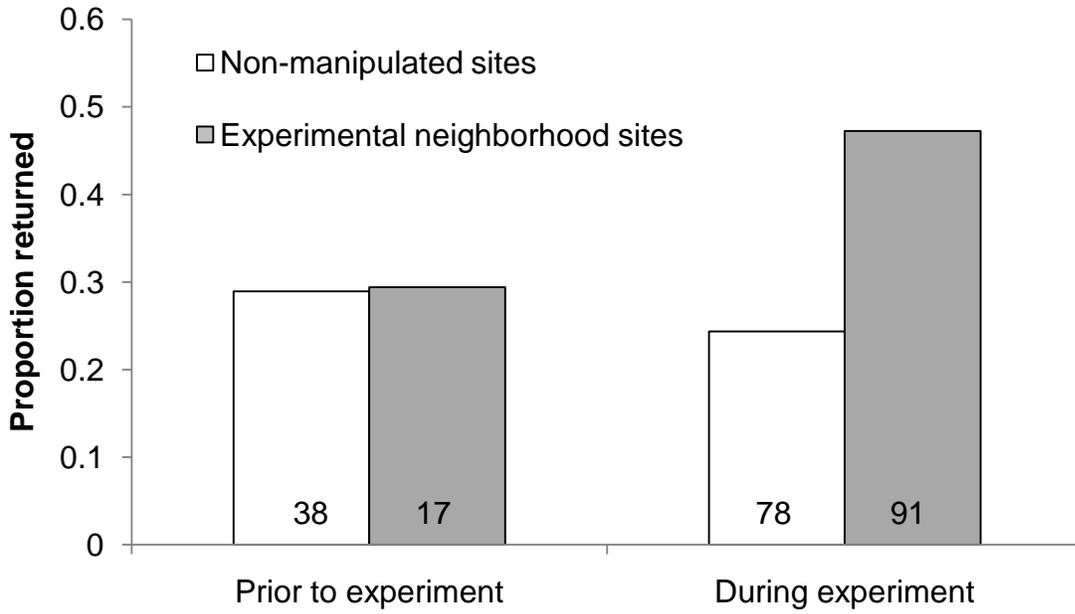


Figure 3-1. Probability that unsuccessful males returned to their neighborhood compared between non-manipulated and experimental sites both pre-manipulation (2000 to 2001) and during the experiment (2002 to 2004). Numbers inside of bars represent sample sizes

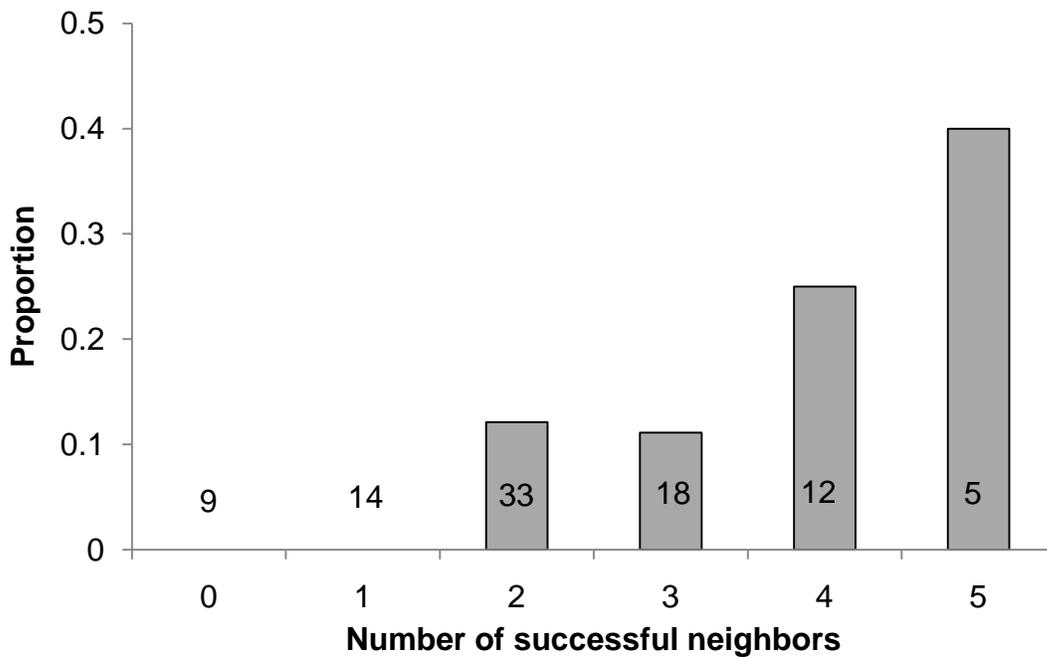


Figure 3-2. Proportion of unsuccessful focal males ($n = 91$) on experimental sites fledging at least one EP offspring compared to number of successful neighbors. Numbers inside of bars represent sample sizes

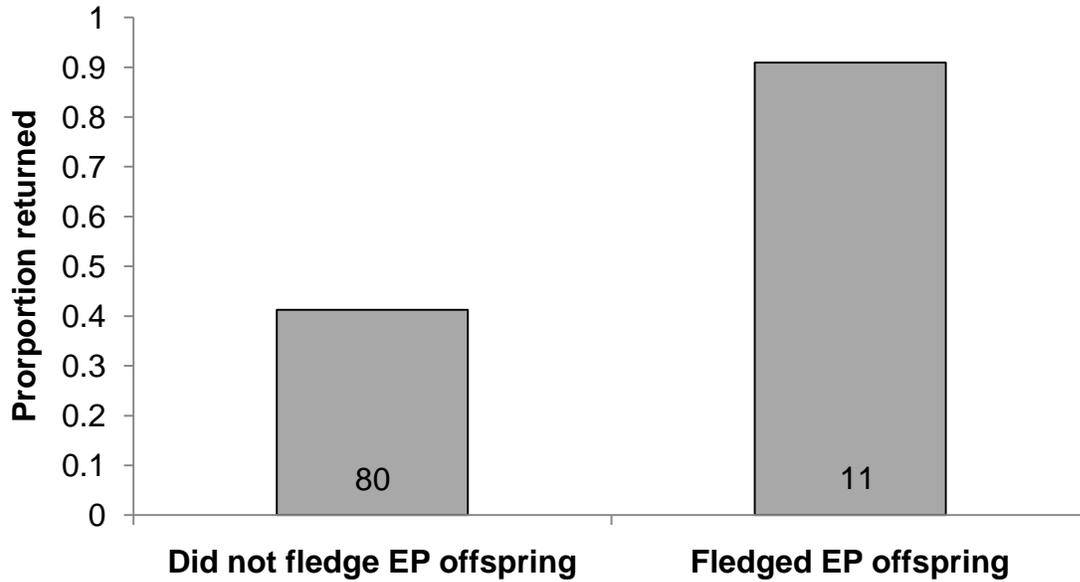


Figure 3-3. Proportion of focal unsuccessful males that returned to their neighborhood the following year after failing or succeeding to fledge at least one EP offspring. Numbers inside of bars represent sample sizes

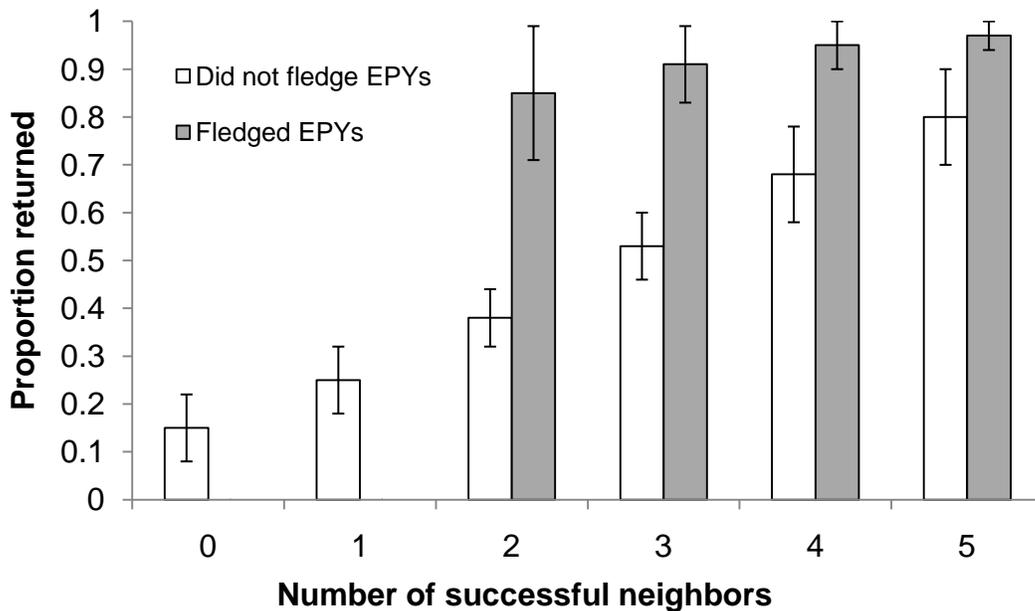


Figure 3-4. Proportion of focal unsuccessful males that returned to their neighborhood compared to success of fledging EP young and the number of successful neighbors. Bars represent mean \pm 1 SE predicted from the final model (see Appendix Figure A-6 for actual proportion of males returned)

CHAPTER 4
FEMALE RELATEDNESS TO SOCIAL MATE INCREASES CUCKOLDRY AND
BETWEEN-YEAR BREEDING DISPERSAL IN A WILD BIRD POPULATION

Introduction

The negative effects of inbreeding, or breeding with relatives, have been widely documented and likely have life-long effects on the fitness of inbred individuals (van Noordwijk 1981; Nieminen et al. 2001; Spottiswoode & Møller 2004; Reid et al. 2005; Marr et al. 2006; Reid et al. 2006; Szulkin et al. 2007; Oh & Badyaev 2008; Charlesworth & Willis 2009). According to long-standing theory, sex-biased natal dispersal or philopatry likely evolved, at least in part, as a means of avoiding inbreeding (Greenwood 1980; Szulkin & Sheldon 2008). Sex-biased natal dispersal is widespread among animals, but recent evidence suggests that, in some systems, natal dispersal is relatively short (Winkler et al. 2005) and insufficient to eliminate all cases of incestuous matings (i.e., first cousin relatedness (r_{xy}) values = 0.125, half-sib r_{xy} = 0.25, full-sib r_{xy} = 0.5) (Hansson et al. 2002; Eikenaar et al. 2008). Clarke et al. (1997) reviewed the existing literature for birds and found a lack of sex-biased natal dispersal in more than half (53%, $n = 39$) of the passerine species surveyed, which supports the idea that, in some systems, patterns of natal dispersal may not have evolved as a direct mechanism to eliminate mating with relatives. Thus several other life-history traits may be involved in avoiding the risks of inbreeding.

Sex-biased breeding dispersal is as widespread among animal taxa as natal dispersal, although it is typically less extensive (Greenwood 1980). For many longer-lived species, breeding dispersal, mate choice decisions, and divorce occur repeatedly throughout their lifetime and likely have equally large effects on individual fitness (Choudhury 1995; Kempenaers et al. 1998; Ramsay 2000; Cockburn et al. 2003;

Foerster et al. 2003; Frommen & Bakker 2006). In addition, breeding dispersal has been shown to be context- or condition-dependent (Chapters 2 & 3) (Switzer 1997; Danchin et al. 1998; Ims & Hjermann 2001; Hoover 2003a; Citta & Lindberg 2007), which suggests that individuals have evolved sophisticated abilities to distinguish between good and bad breeding decisions based on a multitude of cues and information (Doligez et al. 2002). In fact, the ability to avoid pairing or mating with close relatives has been shown to affect both dispersal (Ryberg et al. 2004; Handley & Perrin 2007; Honer et al. 2007) and mate choice in several taxa (Frommen & Bakker 2006; Wheelwright et al. 2006; Archie et al. 2007; Hain & Neff 2007; Lihoreau et al. 2007; Sherborne et al. 2007; Mehlis et al. 2008).

A predisposition for selecting genetically compatible mates should exist if the benefits of doing so outweigh the costs (Mays et al. 2008). Few cases, however, have been found where socially monogamous species avoided pairing with close relatives (but see Cockburn et al. 2003; Wheelwright et al. 2006), because mate choice is confounded by territory choice. In addition to theories regarding social mate choice, dispersal, divorce and inbreeding avoidance, female promiscuity has been offered as a suggested means of alleviating the effects of incestuous pairings if females selectively cuckold social mates that are genetically incompatible (Tregenza & Wedell 2000; Foerster et al. 2003; Mays et al. 2008). In some cases involving several different taxa, authors have suggested that promiscuous pairings have evolved primarily to avoid inbreeding and inbreeding depression (Blomqvist et al. 2002; Tregenza & Wedell 2002; Foerster et al. 2003; Bishop et al. 2007; Fossoy et al. 2008). Although not mutually exclusive, mate choice, breeding dispersal, divorce, and/or extra-pair (EP) mating could

provide an adequate arsenal of behavioral adaptations to diminish or alleviate the effects of pairing with closely related mates. In socially monogamous, territorial songbirds, where female-biased breeding dispersal and EP mating strategies are widespread, however, mate choice is confounded by selection of a breeding territory. In many cases, breeding dispersal has been shown experimentally to be directly affected by territory quality or correlated factors (Haas 1998; Doligez et al. 2002; Hoover 2003a; Parejo et al. 2007). Hence, if reproductive success is largely governed by the effects of nest predation and/or food availability, then choosing a good quality territory may override the benefits of selecting an unrelated mate. Thus, cuckoldry may serve to reduce inbreeding for successful females reluctant to move from a good quality territory, whereas between-year breeding dispersal and divorce in unsuccessful females may prevent both returning to a bad territory and re-pairing with a genetically incompatible mate.

The prothonotary warbler (*Protonotaria citrea*) is a socially monogamous territorial songbird that breeds in secondary cavities in patchily distributed lowland forests throughout the central and southeastern United States (Petit 1999). In my study population in southern Illinois, natal dispersal is not sex-biased and is relatively spatially restricted (i.e., generally < 10 km) (M. McKim-Louder manuscript in prep.). Previous experimental research demonstrated that between-year adult breeding dispersal was reduced for males and females if they successfully fledged offspring (Hoover 2003a). On the rare occasion that successful males did move to a new territory between years, however, females chose their previous territory over their previous social mate (Hoover 2003a). This evidence suggests that territory quality trumps mate choice in this system.

Therefore, successful females may be willing to accept any social mate, regardless of their quality or compatibility, to return to a good quality territory. Hence, these females should have alternative adaptations that alleviate the costs of poor mate choices such as cuckoldry. In contrast, unsuccessful females that are likely to disperse from a bad quality territory may factor in the quality or compatibility of their previous social mate when dispersing between years. Unsuccessful females, which after juveniles are the most dispersive individuals and more likely to disperse from their territory than males (Hoover 2003a; Chapter 2), might disperse farther to avoid re-pairing with a closely related social mate. These factors increase the likelihood that cuckoldry and divorce are necessary adaptations that are related to inbreeding avoidance in this species because sex-biased natal dispersal and mate choice based on past success, which could indicate genetic compatibility, does not seem to prevent or eliminate the effects of poor mate choices on reproductive success.

I now know that female prothonotary warblers cuckold their mates at rates similar to other socially monogamous songbirds (Chapter 3) (Griffith et al. 2002). Although I lack obvious evidence of inbreeding depression, such as reduced hatching success or nestling survival, these effects may be obscured by behavioral mechanisms that alleviate the signs of inbreeding (Archie et al. 2007; Cohas et al. 2008). Collectively, the above-mentioned behavioral and ecological characteristics of my study population make it suitable to investigate whether breeding dispersal decisions, divorce and EP mating strategies are based on female relatedness to their social mate. Unsuccessful females are less likely to return to a territory after a complete breeding failure than successful females (Hoover 2003a); therefore, they should be the most likely individuals to avoid

re-pairing with closely related mates because territory quality does not limit their between-year breeding dispersal. In this study I examined which factors influence cuckoldry and between-year dispersal decisions in female prothonotary warblers. Specifically I tested whether genetic compatibility (i.e., inbreeding avoidance) influenced cuckoldry and whether private information via cuckoldry and/or public information via local conspecific reproductive success influenced patch fidelity and dispersal distances of unsuccessful female warblers.

I conducted a unique experiment to control for the confounding effect of territory quality on mate choice by reducing the perceived quality of warbler territories by causing complete nest failure of randomly selected pairs in my study population. Failed breeders are likely informed about habitat quality on their patch from collecting public information (i.e., conspecific reproductive success) after their own breeding attempts fail (Chapter 2). Thus, to minimize the confounding factor that female between-year breeding dispersal may only be associated with finding a better territory, I attempted to make the majority of neighbors successful. This would ensure that females dispersing beyond the boundaries of their neighborhood pass over several successful territories before deciding on a new mate/territory. These birds use nest boxes that were protected from predation so that I could genetically sample all adults and offspring, but nests of focal pairs were then experimentally depredated to simulate complete reproductive failure for that breeding season. Evidence from previous research suggested that the rates of EP fertilizations were similar to other related species and were generally not skewed towards particular males (Chapter 6). Cuckoldry was apparently random in relation to particular correlates of male age and quality, which suggests that EP matings

are exchanged between males and are more likely to be associated with genetic compatibility and/or variability rather than “good genes” (Akçay & Roughgarden 2007). Thus I predicted that female relatedness to her social mate would influence the probability of promiscuous matings in that season and cuckoldry rate (number of EP offspring/total offspring sampled) would increase with increased relatedness of the social pair. I also tested whether EP sires for those females that cuckolded their mates were less related than their social mates.

Territory quality in my system is relatively predictable between years (Hoover 2003a). Hence, on unsuccessful territories, females should use other information to assess territory or patch quality when making between-year breeding decisions. Previous research showed that patch fidelity of unsuccessful females was related to public information in the form of patch reproductive success (PRS) of conspecifics (Chapter 2). In contrast, male neighborhood fidelity was related to public information in the form of neighborhood success and their own private information related to EP mating success with neighbors (Chapter 3). Therefore, unsuccessful females may also use their own private information in the form of cuckoldry as an indication of either dissatisfaction or incompatibility with their social mate and also the presence of a more preferred or genetically compatible mate. In this instance, I predicted that unsuccessful females will be more likely to return to their patch only if they had information pertaining to other males on the site via cuckoldry. Because mating with closely related social mates could be costly, particularly if females do not have access to a more compatible male via cuckoldry (Foerster et al. 2003), I predicted that relatedness to the social mate

and not cuckoldry would predict the between-year dispersal distances of unsuccessful females.

Methods

Study Area and Study Organism

I conducted this research within the Cache River Watershed in Illinois, USA (37° 18' N, 88° 58' W). I chose four experimental study sites that were discrete patches of forested wetland habitat, each containing at least ten pairs of warblers. I collected additional genetic data during 2002, the first year of the study, from 48 broods on 12 other study sites to compare between experimental and non-manipulated sites. These study sites were separated by at least one kilometer of habitat not suitable for breeding prothonotary warblers and ranged in size from 8 to 73 ha.

The prothonotary warbler is a migratory songbird that winters in Central and South America and breeds throughout the central and eastern United States (Petit 1999). This species is territorial and socially monogamous (Petit & Petit 1996), nests in secondary cavities, prefers to nest over standing water in bottomland and swamp forests (Petit 1999), and readily use nest boxes when available (Petit 1989). Additional details of its natural history and behavior are given elsewhere (Petit 1999; Hoover 2003b, 2006).

Monitoring Individuals and Manipulating Nesting Success

During 2002 to 2004 I monitored color-banded breeding populations of prothonotary warblers using nest boxes made from modified 1.9-L cardboard juice cartons (Fleming & Petit 1986). Methodology for nest box placement, attachment, and spatial arrangement are described elsewhere (Chapter 2) (see Hoover 2003a for additional details of nest boxes and nest monitoring protocol). I captured or re-sighted

all individual warblers. For a more detailed description of capture and banding techniques, and genetic sampling, see Chapters 2 & 3.

During each year from 2002 to 2004 I experimentally manipulated the nesting success of individual pairs on each of the four experimental study so that approximately one-third of pairs each year were randomly assigned to a “failure” group and failed to fledge offspring from their own nest. My target was to assign individual males to the “failure” treatment only once to maximize the number of unsuccessful males for a separate experiment. As a result, a few individual females ($n = 5$) were assigned more than once to the “failure treatment.” For these females, I only used the first year that they were unsuccessful. The remaining pairs (i.e., neighbors) were assigned the “success” treatment (similar to natural levels of reproductive output Hoover 2001) each year and were protected from raccoons (*Procyon lotor*), the main nest predator in the system (Hoover 2003a, 2006), and given the opportunity to fledge as many broods (1 or 2) as possible. I attempted to make all of the neighbors of unsuccessful pairs fledge offspring so that territory quality in the neighborhood was high. Conclusions, therefore, about females dispersing outside of their neighborhood, and thereby dispersing past several previously successful territories, could be interpreted as avoiding re-mating with the same mate in search of a more compatible one, rather than avoiding low-quality territories.

I removed nest boxes from trees and reattached them to two pieces of 1.50-cm-diameter greased conduit placed in the ground and standing one meter away from the original nest tree. Nest boxes placed on conduit were safe from nest predation to control for when predation occurred, and to make sure that I could take blood

samples from all of the nestlings. I then manipulated all nesting attempts of pairs from the “failure” treatment to simulate nest predation and prevent them from fledging any nestlings. For each nesting attempt of the unsuccessful pairs I removed nestlings when they were 4 to 6 days old (they fledge on day 11) and pulled some of the nesting material into the opening of the nest box to mimic nest predation. I relocated these nestlings to the nests of foster parents on other sites not included in the experiment.

I monitored all nesting activity of each individual on every study site and recorded the number of warbler offspring produced by each pair. At the end of each breeding season I had complete information on the identity and reproductive output (warbler offspring fledged) of all warblers breeding on my study sites. To include a variable for local density I counted the number of neighbors for each focal female. Neighbors were defined as warbler pairs with territories adjacent to the focal pair and limited to a radius of three nest-boxes (~160 m) in all directions, which constituted approximately one territory beyond the focal pair.

Documenting Site Fidelity and Local Breeding Dispersal

Each year, I determined the identity of every color-marked individual returning to study sites and captured and color-marked any individuals that were not banded previously. For the purposes of this paper, I focused on the returns of those unsuccessful females that bred on my experimental study sites in the previous year. I determined whether individuals returned to their patch the following breeding season and searched for any dispersing color-marked birds within a 500-m wide area surrounding each study site. During the years of my study, at least half of the nest boxes were unoccupied (Chapter 2).

Microsatellite and Paternity Analyses

For more detailed information regarding handling of DNA and methodology for microsatellite protocols and paternity analyses see Chapter 3. In total, on experimental sites, I identified the sire for 99% ($n = 1462$) of all offspring, including within- and extra-pair, on experimental sites. I was able to identify the sire for 92.2% ($n = 116$) of all extra-pair offspring. Average rates of EP offspring, and broods and males with at least one EP offspring are described elsewhere (Chapter 3). Overall, I observed totals of 279 males ($n = 429$ cases) and 278 females ($n = 424$ cases) on experimental study sites from 2002 to 2004. Mating fidelity was known for 240 of these females (86%) because no offspring were sampled for some pairs that failed in the egg stage or abandoned their nesting attempts prior to the laying of a complete clutch

Relatedness Analyses

For each year of the study, I used eight microsatellite loci to calculate the pair-wise genetic relatedness between females and all males breeding on each patch ($n = 4$). I used the program KINGROUP v 2.0 (Konovalov et al. 2004) to calculate two separate estimators of relatedness (Queller & Goodnight 1989; Wang 2002). Results for each estimator were qualitatively identical; therefore, only the results from the Queller & Goodnight (1989) estimator are reported. An analysis of broods ($n = 25$) containing only within-pair offspring (i.e., full-siblings; expected relatedness value is 0.5) revealed an average relatedness value of 0.51 ± 0.02 (mean \pm SE, interquartile range 0.33 to 0.69), indicating that the Queller & Goodnight (1989) method sufficiently characterized relatedness in my study population.

As a measure of male and offspring heterozygosity I used “internal relatedness”(IR) (Amos et al. 2001) which compares alleles at each locus within an

individual and calculates a relatedness value based on the number of loci that are homozygous and the frequencies of all alleles present in the genotype. The values share similar properties as typical r -values with positive values representing relatively homozygous individuals and negative values for those that are relatively heterozygous.

To determine if females initially avoided settling with closely related social mates I compared the relatedness of social pairs with what was expected based on all male-female dyads within the patch (Reid et al. 2008). I calculated relatedness values for all mating pairs on each site each year and then compared the relatedness of females with their social mate to all other males that were presumed available to that female in that year to serve as the null model. I made the same comparison for those females and their EP mates.

Statistical Analyses

I used data from a total of 69 different focal unsuccessful females where I had information on their social mate. Two of these females cuckolded their social mate with an unidentified EP male and were omitted from any analyses of female relatedness to her EP mate. For 16 females, I was unable to sample any offspring because of weather, cowbird predation, or abandonment. Because I could not evaluate whether these females had or had not cuckolded their social mate, these females were used only for the patch fidelity and dispersal analyses once cuckoldry had been eliminated as a potential explanatory variable. The remaining 53 females that were included in all analyses had a minimum of two offspring sampled (range = 2 to 13). Cuckoldry (yes, no) was defined as finding at least one EP offspring among all of the offspring sampled for a particular female. I used simple chi-square tests to compare the probability of cuckolding their mate for females in the “success” vs. “failure” treatment groups and for

females on experimental and non-manipulated sites. Females typically had one or two EP sires (range = 0 to 3) either in one brood or spread across multiple broods. In the cases where I compared female relatedness to her social male and EP male, I averaged the relatedness values for all EP sires and weighted that average by the number of offspring sired so that there was just one relatedness-to-EP-sires value per female that also accounted for the relative contributions of each EP sire.

For all focal unsuccessful females I calculated the total number of neighbors within their neighborhood (within ~160 m) as a measure of local density because the majority of EP matings occur with neighbors (Chapter 3). Patch reproductive success (PRS) was calculated for each patch each year and included all of the offspring fledged from the site (excluding offspring moved to non-experimental sites) divided by the total number of females breeding on the patch. I tested for site ($n = 4$) and year ($n = 3$) effects on PRS using a simple ANOVA. All of the general population descriptors are reported as the mean \pm 1 SD unless otherwise indicated.

In general, I used generalized linear mixed (GLMM) or general linear mixed (GLM) models using GLIMMIX and MIXED procedures in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) to determine which factors best explained each of the dependent variables. Continuous dependent variables were examined for normality prior to selecting the appropriate model. Because I sampled patches in multiple years I always entered patch identity as a random effect to account for non-independence of cases in all models. I controlled for the number of offspring sampled per female in any GLMM and GLM analyses related to cuckoldry, because the probability of finding one EP offspring increased with offspring sampled. I evaluated the importance of fixed effects using

Wald-type statistics and F-statistics reported by the GLIMMIX and MIXED procedures respectively in SAS and used the ratio of the chi-squared statistic to degrees of freedom to evaluate evidence of over-dispersion ($\hat{c} < 1.2$). Beginning with a full model that included all *a priori* fixed and random effects I used a backward stepwise approach by progressively eliminating non-significant fixed effect variables ($\alpha = 0.05$). I kept any remaining fixed effects with *p*-values less than 0.10. I added interactions to my models only if there was an *a priori* prediction that warranted their inclusion. The statistics reported for all non-significant variables are from adding them to the final model.

To test whether female relatedness to her social mate, female age, the number of neighbors, male internal relatedness (IR), or male and female condition (standardized residuals of mass x tarsus regression, each sex analyzed separately) significantly influenced the probability that a female would cuckold her social mate I used a GLMM with a binomial error distribution (response variable coded as “0” and “1”) and a logit-link function. I included female relatedness to her social mate, number of neighbors (0 to 6), male IR, and male and female condition as scale variables, age [second-year (SY - 1 year old) or after second-year (ASY - at least 2 years old)] as categorical fixed effects. I also included the number of offspring sampled as an additional fixed effect to control for the increased probability of detecting EP offspring.

To determine which factors best explained female patch fidelity I also used a GLMM with a binomial error distribution and a logit-link function. I included cuckoldry (yes, no) and female age, as categorical fixed effects and female relatedness to her social mate, female condition, and the number of offspring sampled as continuous variables. For all GLMMs using a binomial distribution I used the Laplace approximation

method for approximating the likelihood because the penalized quasi-likelihood (PQL) method, the default in SAS, can be biased for binary data (Bolker et al. 2009). For those females that cuckolded their social mate, I used a paired t-test to evaluate whether the relatedness to her EP mate was significantly lower than to her social mate. I also used a Pearson correlation to examine whether the rate of cuckoldry (number of EP offspring/total offspring sampled) increased with an increase in female relatedness to her social mate.

To determine whether cuckoldry decreased the internal relatedness (IR) of offspring I used a total of eight broods from eight different females that contained at least one EP and one within-pair offspring. I fit a linear mixed model using restricted-maximum likelihood (REML) using offspring nested within brood as a random effect and whether the offspring was as a result of an EP mating (yes, no) as a categorical and nestling condition (standardized residuals of tarsus x mass regression) as a scale fixed effect. I also tested whether the scale variables nestling IR, the relatedness of the genetic parents, and/or nestling condition best predicted the return of nestlings to the study system using a GLMM with a binomial error and logit link function.

I fit two separate linear mixed models using REML that included patch identity by year as a random effect using a diagonal covariance structure, and paired as social mates (yes, no) or EP mates (yes, no) as fixed effects to test whether female relatedness to her social or EP mate is similar to what would be expected based on the relatedness of the female to all other potential males on each site each year (male-female dyads). In both models, the patch-by-year random effect was significant and retained in the final model.

To determine whether female relatedness to her social mate influenced her between-year dispersal I used data from those females located in the study system the year after they bred as a focal female ($n = 35$). I estimated breeding dispersal by measuring the distance (to the nearest 5 m) between the approximate centers of the territories (based on the locations of nest boxes used) occupied during the previous and current year. I used a GLMM with a Gamma distribution and log-link function, using PQL to approximate the likelihood, with female relatedness to her social mate, cuckolded (yes, no), female age, PRS, female condition, and the number of offspring sampled as fixed effects and site as the random effect. The Gamma distribution is a positively skewed distribution with values greater than but not equal to zero. To include all individuals (females $n = 35$) in the analysis I added five meters to all dispersal distances so that individuals that returned to their former nest-box would have a non-zero value. For the GLMM for dispersal distance analyses I used the Kenward-Roger adjustment for calculating the degrees of freedom (Kenward & Roger 1997). The Kenward-Roger adjustment is more robust than SAS defaults methods for small sample sizes and uneven block designs (Kenward & Roger 1997; Kowalchuk et al. 2004).

I categorized whether females divorced their social mate in the subsequent year for all females that returned to their previous site where their former mate was present. I then compared the between-year dispersal distances of those females that did and did not divorce to determine if dispersal resulted in divorce. I used a non-parametric Mann-Whitney U-test given that dispersal distances are not normally distributed. For a sub-set of females that divorced ($n = 12$) where I had genetic information for the new social mate I examined whether dispersal was effective at reducing a female's

relatedness to their social mate. I used a non-parametric Wilcoxon signed rank test to test the prediction that divorced females reduced their relatedness to their social mate in year 2 compared to year 1. For all statistical comparisons I report the mean \pm 1 SE unless otherwise indicated.

Results

Focal Females

Of the unsuccessful focal females that attempted at least one brood ($n = 69$), 71%, 26%, and 3% attempted 1, 2, or 3 broods respectively. I genetically sampled a total of 284 offspring from 75 broods of unsuccessful pairs ($n = 53$) and, on average, 5.36 ± 2.35 (mean \pm SD; range = 2 to 13) nestlings per focal female. Of focal females (with ≥ 2 offspring sampled), $32.1\pm\%$ ($n = 53$) cuckolded their mate and for those females that were unfaithful, EP mates sired 1.76 ± 0.83 (mean \pm SD; range = 1 to 4 offspring) of their offspring. The percentage of all females present (focal plus non-focal) that cuckolded their mate in 2002, the first year of the study, did not differ between experimental (13.4%, $n = 127$) and non-manipulated (16.7%, $n = 48$) ($X^2_1 = 0.306$, $p = 0.580$) sites demonstrating that my manipulation did not directly affect the probability of cuckoldry. Of the pairs on experimental sites, unsuccessful focal females ($n = 53$) were not more or less likely to cuckold their social mate compared to females that were successful in their own nest ($n = 187$ females) (unsuccessful = 32.1%, successful = 31.6%) (chi-square; $X^2_1 = 0.05$, $p = 0.942$).

The average patch reproductive success (including only those offspring fledged from the patch) across all years and patches was 2.96 ± 0.77 (mean \pm SD; range = 1.35 to 3.92) offspring/female/patch and did not significantly differ between patches (ANOVA; $F_{3,6} = 1.28$, $p = 0.364$) or years (ANOVA; $F_{2,6} = 1.28$, $p = 0.364$). Females ($n = 53$) had,

on average, 3.0 ± 1.39 (mean \pm SD, range = 1 to 6) actual neighbors, and of those neighbors 2.5 ± 1.15 (range = 0 to 5) were successful in their own nest. The number of actual neighbors represents local conspecific density and potential EP mating opportunities, whereas the number of successful neighbors demonstrates that, on average, females were surrounded by several successful territories. In addition to the 53 females that attempted at least one brood and had offspring that I sampled, I included an additional 16 females to my dispersal distance and social pairing analyses (see below) that had paired, built a nest, and made attempts at breeding, but never made it to the nestling phase.

Social Pairs

In general, I found no evidence that unsuccessful focal females ($n = 69$) avoided pairing with closely related social mates. Females were similarly related to their social mate (mean relatedness \pm SE; -0.003 ± 0.13) compared with all other males breeding on the site in that year (female to all other male dyads; 0.013 ± 0.24) (REML estimation; $F_{1, 2278} = 0.579$, $p = 0.447$). Female relatedness to her social mate, however, did increase the probability of cuckoldry (yes, no) after controlling for the number of offspring sampled (Table 4-1, Figure 4-1). In addition, the overall rate of cuckoldry (number of EP offspring/total offspring sampled/female) increased with female relatedness to her social mate (Pearson's correlation; $r = 0.327$, $n = 53$, $p = 0.017$). Cuckolding females were significantly less related to their EP mates than to their social mates (paired t-test; $t_{15} = 3.68$, $p = 0.002$) (Figure 4-2). Measures of male and female quality and neighborhood density, however, did not influence the probability that a female cuckolded her social mate (Table 4-1).

To examine whether the relatedness of the female to her EP mate was random relative to what was available to her on the patch I compared the relatedness of each female to her EP mate to the average relatedness of the female to all other males on the site that year. Overall, the relatedness of the female ($n = 15$) to her EP sire (mean relatedness \pm SE; -0.022 ± 0.045) did not differ from the relatedness of the female to all other males on the site that year (female to all other male dyads; 0.006 ± 0.013) (REML estimation; $F_{1, 525} = 0.382, p = 0.537$).

For eight mixed broods (within & extra-pair) where I had condition data for all of the offspring, I found that offspring internal relatedness (IR) (i.e., high IR = low heterozygosity) was significantly lower for extra-pair offspring compared to their within-pair brood mates [within-pair IR (mean \pm SE): 0.103 ± 0.036 ; extra-pair: -0.009 ± 0.035] (REML estimation: $F_{1, 34} = 4.932, p = 0.033$). In addition, offspring condition was negatively associated with IR, but the difference was not significant (REML estimation: $\beta\pm SE = -0.055\pm 0.034, F_{1, 34} = 2.721, p = 0.108$). For all offspring from the experiment that were fostered to non-experimental sites 11% ($n = 320$) returned anywhere within the study system. The probability of offspring return decreased with the relatedness of the genetic parents (GLMM, $\beta\pm SE = -2.49\pm 1.04, X^2_{1, 235} = 5.70, p = 0.017$). Neither nestling IR ($\beta\pm SE = -0.62\pm 1.16, X^2_{1, 243} = 0.28, p = 0.598$) nor nestling condition were better predictors of nestling return probability; however, the probability of nestling return did tend to increase with nestling condition ($\beta\pm SE = 0.45\pm 0.25, X^2_{1, 119} = 3.08, p = 0.079$).

Female Dispersal

Unsuccessful females were nearly twice as likely to return to the patch between years if they had cuckolded their social mate compared to if they had not (Table 4-2,

Figure 4-3). No other factor, including patch reproductive success, female age or condition, nor the number of offspring sampled, explained female patch fidelity between years. Those females ($n = 33$) that dispersed within my study system between years, however, dispersed farther from their former territory the more closely related they had been to their social mate after controlling for female condition ($n = 28$ for females with condition scores) (Table 4-3, Figure 4-4). I report the model that included condition scores because female condition only slightly reduced my sample size and did improve the overall fit of the model. The effect of female relatedness to the social mate on dispersal distance (m), however, was qualitatively similar even after condition was removed from the model ($p < 0.05$).

The majority (68%, $n=28$) of the focal unsuccessful social pairs where both the female and male returned to their site between-years ended up divorced. The dispersal distance of divorced females (mean \pm SE; 174.2 ± 31.9) was significantly longer than those that did not divorce (42.2 ± 19.2 m) (Mann-Whitney U-test; $U_{9,19} = 34.5$, $Z = -2.54$, $p = 0.011$). Of those females that divorced between years, and I had genetic information from their new social mate, 75% ($n = 12$) reduced their genetic relatedness to their social mate; however, because of the small sample this relationship was not statistically significant (Wilcoxon signed rank test; $Z = -1.42$, $p = 0.158$) (Figure 4-5).

Discussion

I found strong evidence that unsuccessful female prothonotary warblers exhibit two separate behaviors for reducing their relatedness to their mate(s) and the risks of inbreeding. The first was that females that were more closely related to their social mates were more likely to cuckold them. Females that cuckolded their social mates selected significantly less related EP sires. These EP mate choices, however, did not

differ from what would be expected at random. Cuckoldry rate (proportion of offspring that were EP) increased as a function of female/social-mate relatedness. This behavior resulted in lower internal relatedness for EP offspring, which translated into higher heterozygosity, than their within-pair brood mates. Second, I found that between-year breeding dispersal of unsuccessful females was significantly affected not by public information in the form of patch reproductive success, but by their own private information about their relatedness to their social mate and whether they had cuckolded them or not. Females that cuckolded their social mates were nearly twice as likely to return to their patch between years compared to females that had not. Those that returned, however, dispersed farther between years from their territories the more related they had been to their social mate, regardless of whether or not they cuckolded them. Longer dispersal distances were associated with divorce and the majority of females that divorced effectively decreased their relatedness to their new social mate relative to their social mate in the previous year.

Extra-Pair, Relatedness and Mate Choice

As reported in several other studies (Blomqvist et al. 2002; Foerster et al. 2003; Eimes et al. 2005; Freeman-Gallant et al. 2006; Stapleton et al. 2007; Cohas et al. 2008), female prothonotary warblers were more likely to cuckold their social mate with an increase in relatedness, which supports the idea that EP copulations may be a mechanism to avoid inbreeding. Several studies have shown that EP matings result in offspring with higher individual heterozygosity that may in turn also lead to higher fitness in relation to disease (Hawley et al. 2005), more elaborate secondary sexual traits (Foerster et al. 2003), and increased recruitment (Hansson et al. 2001). Thus, because heterozygosity was higher for EP offspring relative to their brood mates, I expected that

their condition would also be higher. Although not statistically significant, EP offspring tended to be larger (corrected for body size) than their within-pair (WP) brood mates. This lack of a significant effect may be a result of a small sample size, but may also reflect variation caused by other environmental factors. In my system, *Protocalliphora* sp. blowflies are a common nest parasite (W. Schelsky unpublished data), which have been shown to diminish or reduce the differences between EP versus WP offspring quality in the tree swallow (*Tachycineta bicolor*) (O'Brien & Dawson 2007). I would need more data on nestling condition, growth rates, rates of blowfly infestation, and other measures of nestling quality to determine whether EP offspring are indeed better quality and have a fitness advantage relative to WP offspring. For all within- and extra-pair offspring raised with foster parents during the experiment, however, the relatedness of the genetic parents best predicted the return of offspring and returning offspring tended to be in better condition which suggests that there is some fitness benefit of mating with a less closely mate and nestling condition may also be a reasonable indication of nestling quality. Although a measure of microsatellite heterozygosity, internal relatedness based on loci from this study, may not be indicative of genome-wide heterozygosity (Masters et al. 2009), or heterozygosity, *per se*, is less important than overall genetic compatibility of the parents.

I did not find evidence that females avoided pairing with closely related social mates, which suggests either females cannot determine their relatedness to particular males, or females prefer a particular territory regardless of which male is present. Past research showed that successful females that had a choice between their former territory and mate always chose the territory (Hoover 2003a), which indicates that the

territory is more important to their reproductive success than their mate. Females would have to be more selective of their social mates than their territories to expect a pattern associated with avoidance of close relatives for social pairs. Variation in reproductive success in my system is largely governed by nest predators (Hoover 2006) and the brown-headed cowbird (*Molothrus ater*), a brood parasite (Hoover 2003b; Hoover & Reetz 2006; Hoover & Robinson 2007) and to some extent blowflies (W. Schelsky, unpublished data). Hence, if females choose good territories and cuckold their mates, they will likely be more productive than by choosing a compatible mate on a poor quality territory. Alternatively, females may choose territories over mates because they may not be able to immediately recognize closely related individuals which may result in errors in choosing the most compatible mate.

Females, however, were less related to their extra-pair mates than their social mates, which could indicate that females solicit EP males after they have had time to assess their familiarity or relatedness to their social mate. The EP sires that females “chose” did not differ from all of those males available to them on the patch. Therefore, females may eventually recognize that their social mate is closely related to them and seek EP copulations from any other available male. There is evidence that, in some species, recognition of known individuals, such as a former mates or siblings raised together exists (Palestis & Burger 1999; van der Jeugd et al. 2002; Cockburn et al. 2003), but these patterns have been typically found in colonial and cooperative species where relatives are more likely to interact (Komdeur 1999). The idea of kin recognition in birds is controversial because most kin recognition documented in the animal world involves chemical signaling detected by olfaction or other sensory modes (Nakagawa &

Waas 2004), which are reduced or non-existent in some avian species. In prothonotary warblers, females may recognize former brood mates or older offspring as a result of familiarity or phenotype, and therefore reduce their chances of pairing or mating with some kin (i.e., siblings) but much research is needed on potential mechanisms of kin recognition.

Females could also be seeking copulations with familiar males, such as former social and/or EP mates. Thus females end up copulating with familiar males that were genetically compatible in the past. Previous research showed that male prothonotary warblers can increase their probability of EP mating success by returning to a familiar neighborhood (Chapter 6), which suggests that males also play an active role in seeking EP copulations. Both experience (i.e., site familiarity) and age, which is often correlated, may contribute to EP success of males. For example, Kleven et al. (2006) found that older male reed buntings (*Emberiza schoeniculus*) were more likely to foray into neighboring territories and sire more EP offspring. In my study system, males with breeding experience on a particular site, regardless of age, were more successful at gaining EP fertilizations than males without experience (Chapter 6). By returning to the same site between years, males may encounter familiar EP females or social mates who may choose them again for EP mating. For males that gained EPFs in two consecutive years, however, none of them were with the same females (Chapter 6), which shows that male EP mating success is not simply because familiar females favor them. Therefore, males can increase their chances for EP copulations by returning to large and familiar neighborhoods regardless of the females present, and it is possibly

post-copulatory mechanisms rather than direct female choice of particular males that select the EP sire.

The most parsimonious explanation for why females find less related EP sires is that females, in general, are promiscuous and post-copulatory mechanisms involved with sperm competition, genetic compatibility, and/or cryptic female choice (Zeh & Zeh 1997; Jennions & Petrie 2000; Griffith & Immler 2009) determine which males sire the most offspring. Although I lack data on copulation and fertilization rates, these mechanisms are unlikely to be operating in my system. Although EP fertilizations could be the end result of both multiple copulations with several males and sperm competition or cryptic choice, previously I found strong experimental evidence that males were aware of their EP mating success and somehow knew whether those offspring fledged (Chapter 5). This suggests that males either can recognize their own offspring, or copulations are rare enough to provide an honest signal of EP mating success. Whether females that are more closely related to their social mates seek EP copulations at a higher rate is unknown, but future work should focus on the active roles of both males and females in EP copulations as well as the ability to recognize closely related kin.

Several hypotheses exist for why females seek EPFs (Jennions & Petrie 2000). Good genes promote female preferences for high quality males that would in turn produce good quality and/or more attractive offspring. Because I did not measure any sexually selected traits such as crown color or ultra-violet pigmentation that may indicate “good”, “viability”, or “attractiveness” genes I cannot rule out the possibility that females may also be choosing more attractive or better quality males. The social males’

condition, a common measure of quality, however, did not predict the probability that a female cuckolded him.

Alternatively, females that choose more heterozygous males could produce offspring that are more heterozygous, which in some studies led to higher fitness correlates (Hansson et al. 2001; Foerster et al. 2003; Hawley et al. 2005). Male heterozygosity in this study had no effect on the probability a female cuckolded him after controlling for relatedness of the social pair. If the parents are closely related, regardless of male heterozygosity, then the offspring will be more likely to inherit the same alleles from each parent resulting in more genome-wide homozygous offspring.

Genetic compatibility, the idea that each female has an ideal genetic partner, which tends to result in a “trading” of EP offspring between males rather than a high reproductive skew for males with “good genes” (Akçay & Roughgarden 2007), however, best fits the pattern of EP fertilizations in my system I found no evidence that any particular group of males (e.g., old or young, large or small, high or low heterozygosity) was more or less likely to be cuckolded, and males that received EP fertilizations were just as likely to be cuckolded as all other males (Chapter 6). All of this evidence suggests that EP sires are being selected more for compatibility rather than for “good genes” or heterozygosity. There is a precedent, however, for finding evidence that both selection of showy traits and genetically compatible males can co-occur in the same population (Oh & Badyaev 2006).

In addition to compatible genes, females could be receiving additional benefits from mating with extra-pair mates. Females could increase the genetic diversity between offspring by “genetically bet hedging”. Genetic bet hedging may be important in

highly variable systems where one genotype is not superior over others and it would be difficult for females to identify males with the most viable genes for the future (Jennions & Petrie 2000). Extra-pair matings in turn could provide insurance that at least some of her offspring would survive to reproduce. If genetic bet hedging was the mechanism promoting female promiscuity, then those females that cuckold their mates should have more offspring recruited to the population regardless of which male sired them. For females in this study, however, those that did not cuckold their mate produced more recruits per year than those that did cuckold their mates (did not cuckold mate = 0.52 ± 0.07 recruits/year, cuckolded mate = 0.07 ± 0.07 recruits/year; GLMM, Poisson error, log link, $\beta \pm SE = 2.34 \pm 1.10$, $X^2_{1, 44} = 4.58$, $p = 0.032$) after controlling for relatedness of the social pair, and the number of offspring sampled per female. This suggests that increased overall genetic diversity between offspring via cuckoldry does not promote higher recruitment of offspring.

Dispersal and Divorce

Unsuccessful female prothonotary warblers that cuckolded their social mate were nearly twice as likely to return to their patch between-years compared to unsuccessful females that did not cuckold. Previous research showed that unsuccessful females returned to their patch based on public information in the form of patch reproductive success (PRS) (Chapter 2); however, private information via cuckoldry was not included in that study. Although I had a relatively wide range of PRS values (1 to 4 offspring/female/patch/year), I may have had inadequate power to find two significant main effects in my model. It could be that if PRS is at some minimum threshold, females switch to their own private information pertaining to cuckoldry and that PRS works well at a coarse scale (Doligez et al. 2002) to help differentiate between

sources and sinks (Pulliam & Danielson 1991) rather than between good versus better patches.

Unsuccessful females may also be more likely to return to their patch given that they have some private information pertaining to other males on the site. If sampling (Wagner 1998; Wagner & Danchin 2003) and identifying a compatible or familiar mate is important, then unsuccessful females may choose to return, but move away from the previously related mate to avoid re-pairing. In fact, females increased their between year dispersal distance with relatedness to their previous year's social mate regardless of cuckoldry. Females are not necessarily moving far just to choose a better territory, because in my experiment I increased the success of neighbors, which did not influence dispersal distance (Table 4-3). Thus, females that moved outside of their neighborhood (i.e., > ~160m) between years would have passed over several previously-successful territories before they settled. Taken together, my results suggest that females may be unable to initially determine whether or not a new prospective mate is closely related.

Females do, however, make subsequent adjustments based on their relatedness to their social mate via cuckoldry within the breeding season and dispersal between breeding seasons when mated to a closely related male. Hatching failure and/or offspring quality, such as condition or begging intensity, and/or nestling death, may provide clues to females about her genetic compatibility to her social mate. In fact, for females that did not cuckold their mates ($n = 35$), hatching failure increased with relatedness to their social mate (GLMM, Poisson error, log link; $\beta \pm SE = 2.90 \pm 0.83$, $X^2_{1, 32} = 12.12$, $p < 0.0001$) after controlling for the total number of eggs that were laid ($\beta \pm SE = 0.21 \pm 0.07$, $X^2_{1, 44} = 7.89$, $p = 0.005$). Future experiments are needed to

ascertain whether cues from hatching failure, offspring quality, and/or recognition of relatedness to mates during earlier breeding attempts influences cuckoldry and between year breeding dispersal.

Dispersal distances were longer for females that divorced compared to those that did not divorce, but were relatively short compared to natal dispersal, suggesting that relatively short-distance breeding dispersal (i.e., < 1km) may be adequate to avoid re-pairing with an incompatible mate the next breeding season. Females that divorced, and for which I had genetic information from their next social mate, tended to find a less related social mate. For those females where their relatedness to their social mate was > 0.05, all but one left their former territory, and the majority dispersed beyond the borders of their neighborhood. In these cases, females could limit their interactions with their previous social mate given that, in related species and this one (Chapter 3), EP mating and interactions tend to occur with neighbors (Stutchbury et al. 1994; Yezerinac et al. 1995; Perreault et al. 1997; Pedersen et al. 2006). Because females that dispersed between years were more closely related to their social mate on average, it is likely that finding a less-related mate in the subsequent year happened by chance. Interestingly, two of the females that divorced increased their relatedness to their new social mate relative to the previous year's mate. In fact, these females' relatedness to their social mates were on the far, low end of the relatedness spectrum (i.e., < - 0.1), which may suggest a level of optimal genetic similarity (Nakagawa & Waas 2004; Cohas et al. 2008). The fact, however, that dispersal distance varied non-randomly with female relatedness to her social mate is certainly suggestive that some other information may be involved.

Conclusions

Natal dispersal in my system does not appear to be sufficient to reduce all incestuous matings (i.e., first cousin relatedness (r_{xy}) values = 0.125, half-sib r_{xy} = 0.25, full-sib r_{xy} = 0.5) and breeding dispersal in unsuccessful females was associated, at least in part, with avoiding being mated to the same closely related males in the subsequent year. Because territory quality is relatively predictable between years (Hoover 2003a, 2006), females that were unsuccessful and dispersing from a bad territory likely have lower costs associated with switching territories than those that had been successful. Successful females may not disperse from closely related males in the same way, unless cuckolding their social mate is also costly (i.e., loss of male parental care contributions *sensu* Moller 1988, 1991). Breeding dispersal in successful females may occur only when the benefits of returning to a good quality territory are outweighed by the costs of re-mating with a closely related social mate. Future research will focus on the costs and benefits of breeding dispersal decisions for successful females to determine whether dispersing away from closely related males is a widespread phenomenon in my system. The results of this study make it clear that females used cuckoldry within-season and breeding dispersal between seasons to alleviate or avoid being mated to a closely-related male. How and when females know the relatedness of their social mate has yet to be determined.

Table 4-1. Results of GLMM (binomial error and logit link function) on the probability female prothonotary warblers ($n = 53$ females) cuckold their social mate in relation to relatedness of the social pair, condition of social mate, internal relatedness (IR) of social mate, female condition, number of offspring sampled, female age, and the number of neighbors. Estimate for the random effect* of patch identity is from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Number of offspring sampled	$X^2_{1,44} = 6.12$	0.573 \pm 0.232	0.013
Relatedness to social mate	$X^2_{1,44} = 5.38$	6.129 \pm 2.643	0.020
Patch identity*	$Z = 0.77$	1.122 \pm 1.461	0.221
Removed variables			
Age	$X^2_{1,43} = 0.47$		0.492
1 year old		0.677 \pm 0.987	
2+ years old		0	
Social male IR	$X^2_{1,43} = 0.02$	-0.379 \pm 2.645	0.886
Social male condition	$X^2_{1,24} = 0.04$	-0.345 \pm 0.479	0.847
Female condition	$X^2_{1,33} = 0.00$	-0.022 \pm 0.336	0.949
Number of neighbors	$X^2_{1,42} = 0.00$	0.021 \pm 0.348	0.952

^a Estimates are on a logit scale. Estimates of removed variables are from when they were added alone to the final model.

Table 4-2. Results of GLMM (binomial error and logit link function) on the probability of between-year patch fidelity of unsuccessful female ($n = 53$ females) prothonotary warblers in relation to public and private information. Estimates for the repeated measures random effect* of patch identity by year are from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Cuckolded mate	$X^2_{1,45} = 4.60$		0.032
No		-1.540 \pm 0.718	
Yes		0	
Removed variables			
Number of offspring sampled	$X^2_{1,44} = 0.68$	0.125 \pm 0.151	0.411
Age	$X^2_{1,44} = 2.50$		0.114
1 year old		-1.155 \pm 0.731	
2+ years old		0	
Patch reproductive success	$X^2_{1,44} = 0.52$	-0.345 \pm 0.479	0.472
Female condition	$X^2_{1,34} = 0.21$	-0.125 \pm 0.271	0.645
Patch identity*	-----	0	-----

^a Estimates are on a logit scale. Estimates of removed variables are from when they were added alone to the final model.

Table 4-3. Results of GLMM (Gamma error and log link function) for between-year dispersal distance (m) of female prothonotary warblers ($n = 28$ females) in relation to relatedness to social mate, female condition, female age, patch reproductive success, and female cuckolded mate (yes, no). Estimate for the random effect* of patch identity is from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Relatedness to social mate	$\chi^2_{1,25} = 8.22$	2.929 \pm 1.021	0.004
Female condition	$\chi^2_{1,25} = 3.26$	0.254 \pm 0.141	0.071
Patch identity*	$Z = 3.54$	0.923 \pm 0.261	<0.001
Removed variables			
Cuckolded mate	$\chi^2_{1,22} = 0.35$		0.556
No		-0.221 \pm 0.375	
Yes			
Patch reproductive success	$\chi^2_{1,24} = 0.20$	-0.135 \pm 0.304	0.658
Number of offspring sampled	$\chi^2_{1,24} = 0.10$	-0.023 \pm 0.073	0.756
Number of successful neighbors	$\chi^2_{1,24} = 0.06$	0.043 \pm 0.171	0.800
Age	$\chi^2_{1,24} = 0.01$		0.923
1 year old		0.044 \pm 0.450	
2+ years old		0	

^a Estimates are on a log scale. Estimates of removed variables are from when they were added alone to the final model.

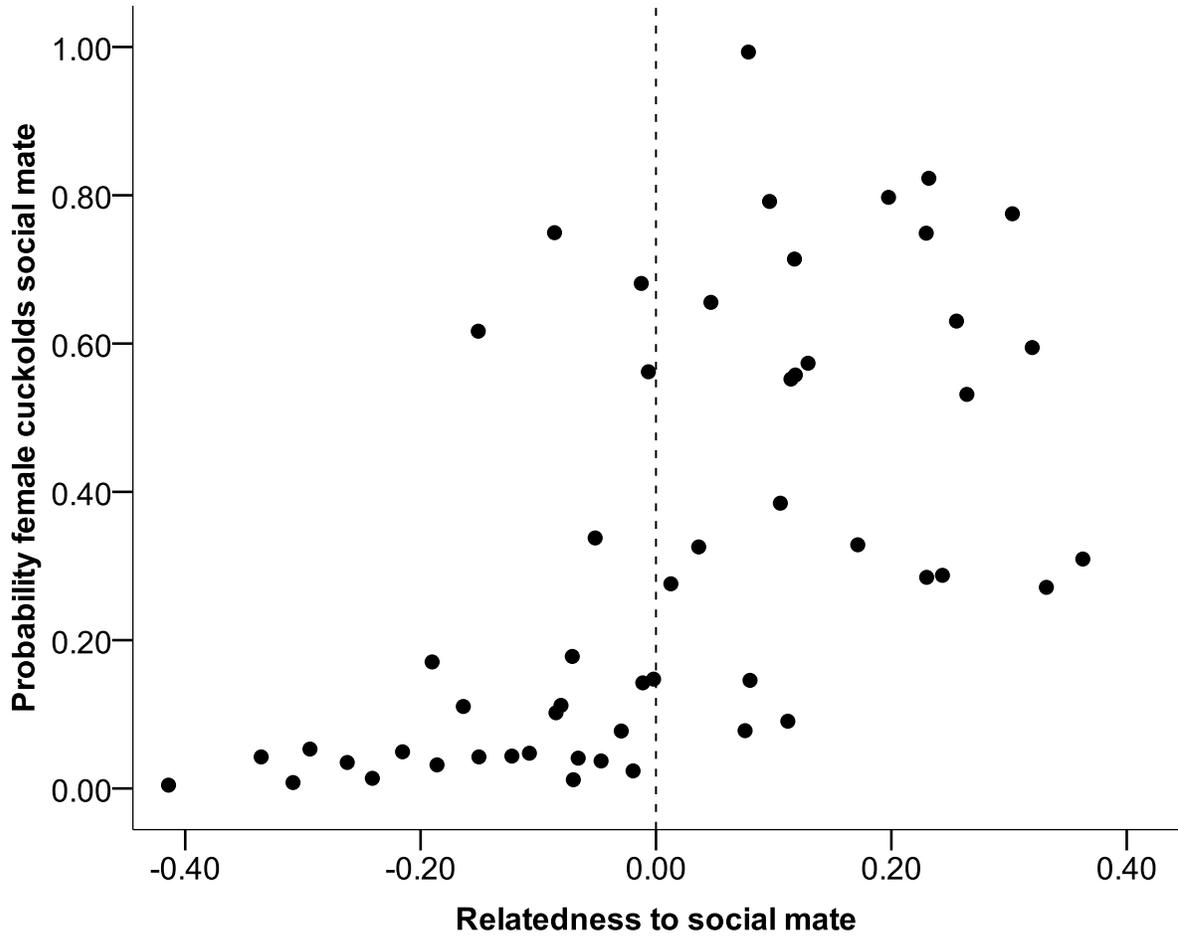


Figure 4-1. Model estimates of the probability that a female cuckolds her social mate based on their pair-wise relatedness (r)

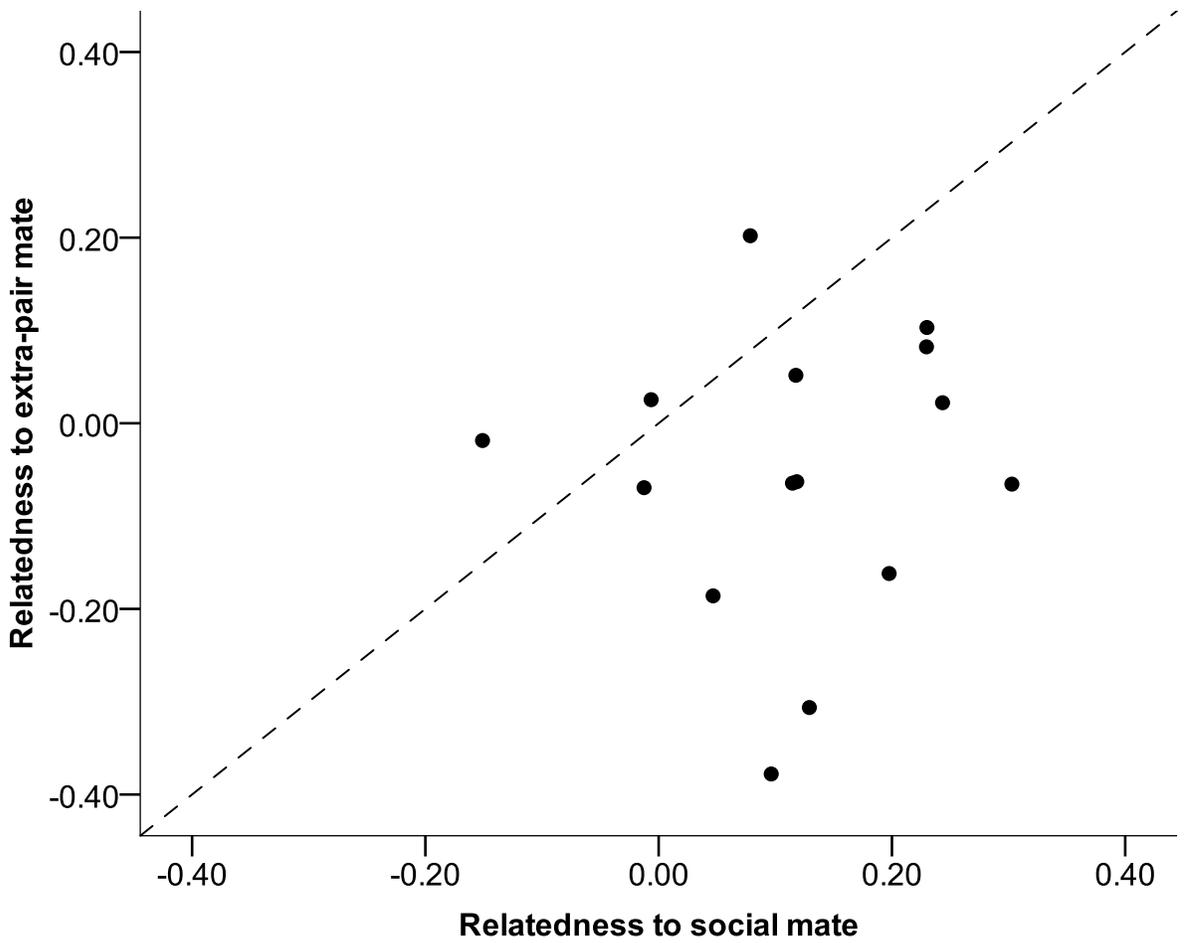


Figure 4-2. Pair-wise comparisons of females' relatedness to their EP mates versus their social mates. Dotted line represents no difference between the two values. Values below the line represent those females whose relatedness to their EP mate was lower than their social mate

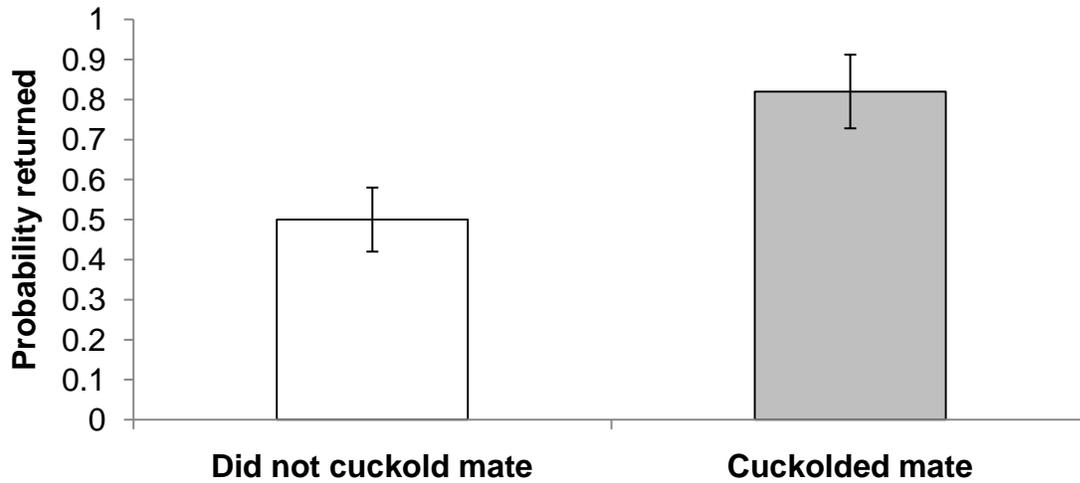


Figure 4-3. Model estimates (mean \pm SE) of probability of between-year site fidelity for females based on whether or not they cuckolded their social mate in the previous year (see Appendix Figure A-7 for actual proportion of females returned)

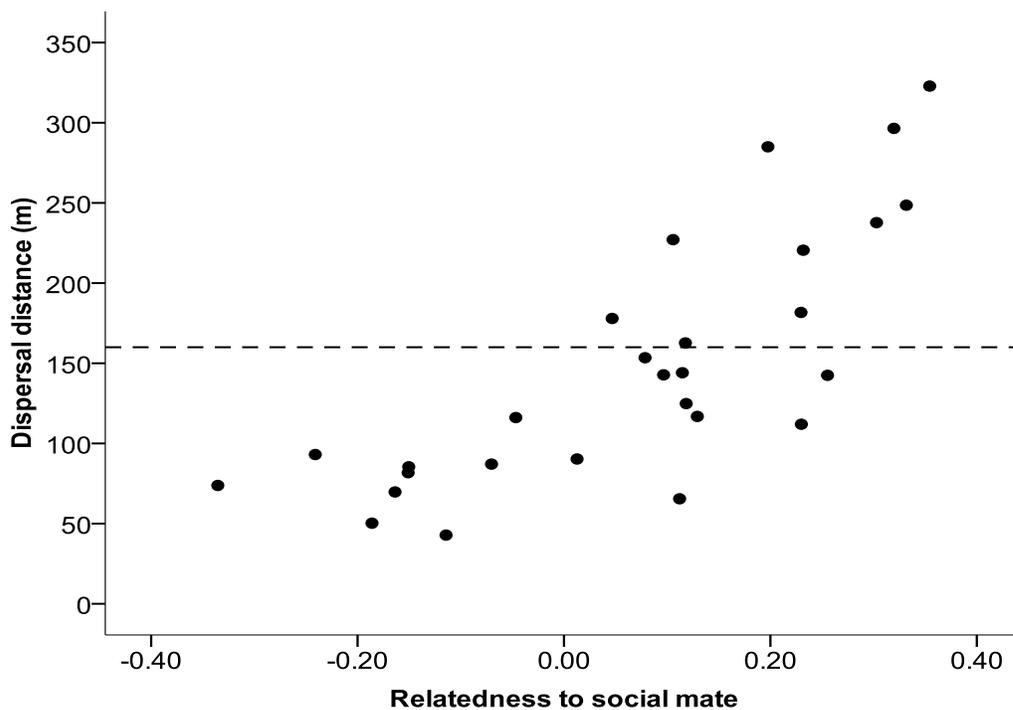


Figure 4-4. Model estimates of the distances moved (m) between years by unsuccessful female prothonotary warblers based on their relatedness to their social mate in the previous year. Dotted line indicates the approximate distance to her former neighborhood's boundary (see Appendix Figure A-8 for actual distances moved (m) between years by returning females)

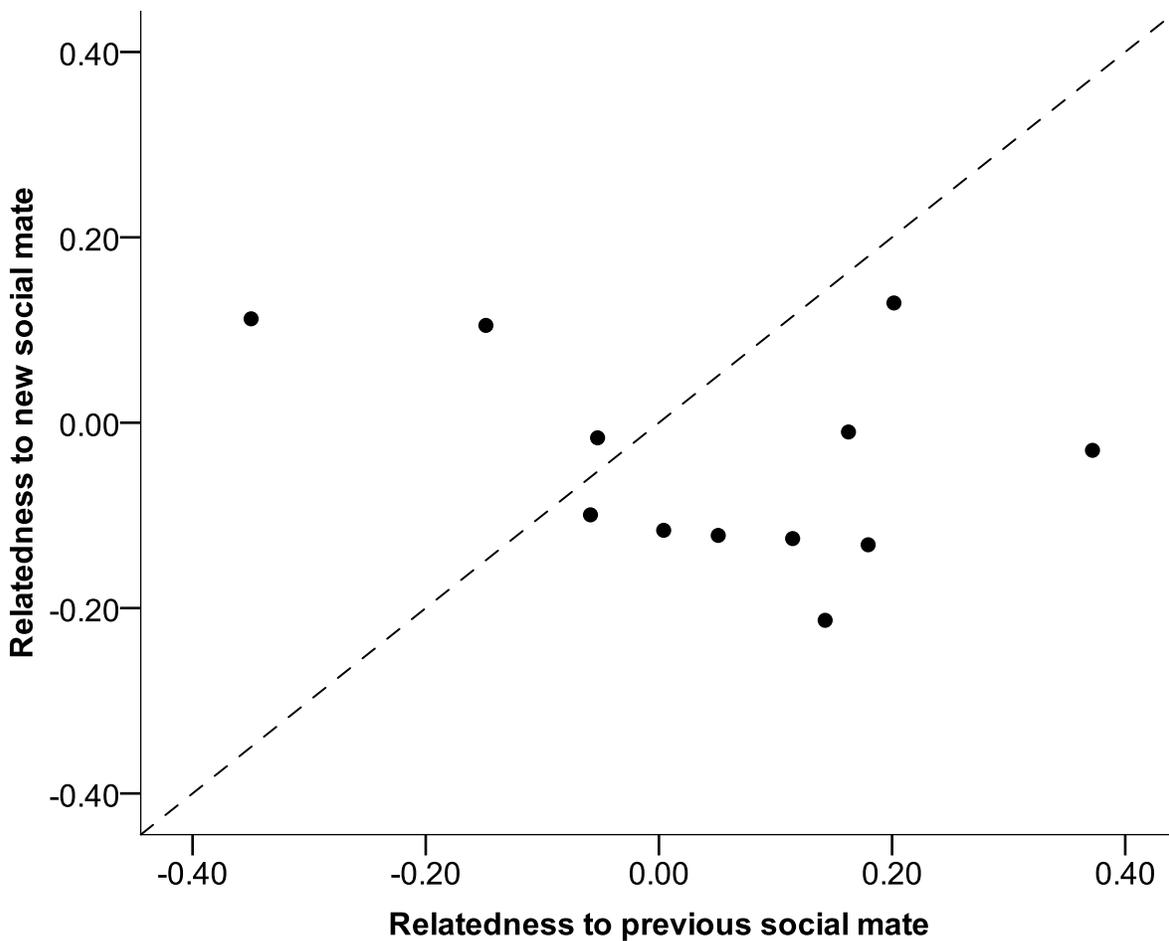


Figure 4-5. Pair-wise comparisons of females' relatedness to their previous social mates versus their new social mates after dispersing between years. Dotted line represents no difference between the two values. Values below the line represent those females whose relatedness to her new social mate was lower than her previous year's social mate

CHAPTER 5 EXPERIMENTAL EVIDENCE THAT MALES MONITOR THE OUTCOME OF THEIR EXTRA-PAIR OFFSPRING

Introduction

The dispersal, movement and spatial distributions of males and females are often in direct relation to mating opportunities (Emlen & Oring 1977; Wikelski et al. 1996; Carranza 1999; Wagner & Danchin 2003; Williams & Rabenold 2005; Lane et al. 2009). In socially monogamous songbirds, mating success due to extra-pair (EP) opportunities often creates significant variation in male realized reproductive success (i.e., total offspring produced = fledged from own nest - lost to cuckoldry + EP young fledged from neighboring nests) (Webster et al. 1995; Yezerinac et al. 1995; Stutchbury et al. 1997; Sheldon & Ellegren 1999; Albrecht et al. 2007) and potentially provides opportunity for sexual selection of traits or behaviors. A male's competitive ability in obtaining EP mates is often relative to other males (Pedersen et al. 2006; Chiver et al. 2008) and in many species these EP mating opportunities tend to be with neighbors (Stutchbury et al. 1994; Perreault et al. 1997; Stutchbury 1998; Webster et al. 2001; Pedersen et al. 2006). Thus, neighbors can either positively or negatively influence a male's realized reproductive success. Indeed, there is some evidence that, within species, density can influence rates of EP (Gowaty & Bridges 1991; Griffith et al. 2002).

Dispersing to or from locations where individual rates of EP are high or low should only occur if individual males can accurately assess their own reproductive success including not only whether they sire EP offspring but also discerning whether those offspring fledge. Bad decisions could actually reduce fitness if it results in either lost paternity without reciprocal gains in EP offspring or failure to fledge offspring as a result of poor habitat quality. Hence, dispersal decisions should be based on information that

accurately predicts a male's realized reproductive success. It is known that, in many species, an individual's own reproductive success with their social mate influences dispersal decisions (Haas 1998; Doligez et al. 2002; Hoover 2003a). What is not known is if males are aware of their own EP mating success and can correctly identify favorable EP mating opportunities where they not only gain EP copulations (EPCs), but also EP fertilizations (EPFs) that result in fledged offspring (EPYs).

Evidence exists that males in some species can correctly ascertain their share of paternity in their own nest and correspondingly contribute less parental care if they suspect mate infidelity [(Arnqvist & Kirkpatrick 2005) and the references therein]. If male EP mating success significantly increases a male's realized reproductive success and reproductive variance among males, then there should be selection on a male's ability to recognize conditions that either increase or decrease their overall success. The degree of female promiscuity in most species is unknown. In some cases, EPCs may rarely occur (Michl et al. 2002), or EPCs are common and post-copulatory mechanisms such as sperm competition or cryptic choice by females may sort out the sires of their offspring (Birkhead & Møller 1998; Griffith 2007; Griffith & Immler 2009). There is also evidence of direct and indirect selection against female promiscuity (Arnqvist & Kirkpatrick 2005, 2007) that may contribute to significant variation in EPCs and EPFs among species. Amidst the variation in rates of EP paternity (Griffith et al. 2002) and presumably rates of EPCs, it is no surprise that males may not always be certain of their EP mating success.

In this study, I exploited a newly identified behavioral response to EP mating success of socially monogamous, territorial male prothonotary warblers (*Protonotaria*

citrea) in order to test whether males can identify favorable EP mating opportunities. I showed in a previous study that unsuccessful males gaining EPYs with neighbors returned between years to their neighborhood at more than twice the rate of those males without EPYs (Chapter 3). What was uncertain was whether males that had EPYs returned because they simply gained EPCs/EPFs with a female or whether they were aware of their realized reproductive success (EPYs) (i.e., fledged EP offspring) (Chapter 3).

To determine whether male prothonotary warblers have the ability to discern between EPCs/EPFs versus EPYs, I specifically investigated whether the realized reproductive success and dispersal decisions differed for three experimental categories that were based on the degree of EP mating success. The first two categories were randomly selected from an experimental population and included males that: 1) produced EPYs, and 2) had EPFs that did not fledge (EPFs no EPYs). The third category included males without any EP mating success (no EPFs) to serve as a control. I randomly manipulated pairs of warblers such that some pairs were successful in their own nests (“success treatment”) and others failed to fledge their own offspring (“failure treatment”). As a result, males with EPFs in neighboring nests would fledge them only if that particular neighbor was successful in that particular nesting attempt. I focused on the between-year neighborhood fidelity of males in the “success” treatment because they represented the largest sample size and still allowed me to control for the success within their own nests.

I tested whether males responded to their EP fledging success by returning to their neighborhood. I predicted that males that had at least one EPY would have a higher

realized reproductive success than those with EPFs but no EPYs and those with no EPFs. Past research in this system showed that females cuckolded their males based on their relatedness to her social mate rather than some measure of quality (Chapter 4) and cuckoldry was randomly distributed across groups of males based on mass (size-corrected), age, and male EP status (Chapter 6). Because my previous measures of quality did not indicate an advantage in EP mating success for particular males and males were randomly chosen to produce EPYs, I did not consider male quality a confounding factor in my experiment. If EPCs were an important indicator to males of their EP mating success, then I would expect that males with EPYs and males with EPFs but no EPYs would return to their neighborhoods at similarly high rates and at rates higher than those males with no EPFs. This prediction is based on the assumption that EPCs are correlated with EPFs (see both references for opposing views on this debate: (Arnqvist & Kirkpatrick 2005; Griffith 2007)). If, however, males are fully aware of their actual EPYs, then males with EPYs would return to their neighborhoods at higher rates than both of the other treatment groups.

Methods

Study Area and Study Organism

I conducted this research on a long-term (15 years) study population of prothonotary warblers (*Protonotaria citrea*) in the Cache River Watershed in Illinois, USA (37° 18' N, 88° 58' W). I chose four experimental study sites (10 to 44 ha) each containing at least ten pairs of warblers that were in discrete patches of forested wetland habitat and were separated from each other by at least one kilometer of habitat not suitable for breeding prothonotary warblers.

The prothonotary warbler is a migratory songbird that winters in the Neotropics and breeds in the central and eastern United States (Petit 1999). This species is territorial and socially monogamous (Chapter 3) nests in secondary cavities and has rates of extra-pair offspring similar to other socially monogamous songbirds (Griffith et al. 2002). Prothonotary warblers prefer to nest over water (Petit and Petit 1996) and readily use nest boxes when available (Petit 1989; Blem & Blem 1994; Hoover 2003a). Additional details of its natural history and behavior are given elsewhere (Petit 1999; Hoover 2003b, 2006).

Monitoring Individuals and Manipulating Nesting Success

During 2002 to 2004 I monitored breeding populations of color-marked prothonotary warblers using nest boxes made from modified 1.9-L cardboard milk cartons (Fleming & Petit 1986). Methodology for nest box placement, attachment, and spatial arrangement are described elsewhere (Chapters 2 & 3) (see Hoover 2003a for additional details of nest boxes and nest monitoring protocol). I captured or re-sighted all individual warblers each year. For more detailed description of capture techniques and genetic sampling, see Chapters 2 & 3.

During each year I experimentally manipulated the nesting success of individual pairs on each of the four experimental study sites so that approximately 33% of pairs each year were randomly assigned to a “failure” group and failed to fledge offspring from their own nest. The remaining pairs were assigned the “success” treatment and were protected nest predators (Hoover 2003a, 2006), and encouraged to fledge as many broods (1 or 2) as possible. I removed nest boxes from trees and reattached them to two pieces of 1.50-cm-diameter greased conduit placed in the ground and standing one meter away from the original nest tree. Not all boxes had to be moved every year;

however there was no evidence of an effect of box disturbance on individual return rates and/or behavior (Chapter 2). Nest boxes placed on conduit were safe from nest predation so that I could control when predation occurred and to make sure that I could take blood samples from all of the nestlings. I then manipulated all nesting attempts of pairs from the “failure” treatment to simulate nest predation and prevent them from fledging any nestlings. For each nesting attempt of the unsuccessful pairs I removed nestlings when they were 4 to 6 days old (they fledge on day 11) relocated these nestlings to the nests of foster parents on other sites not included in the experiment.

Aside from individual reproductive success of males within their own nests, the manipulation also influenced the number of successful neighbors and the fledging or not of extra-pair offspring in neighboring nests. The degree of EP mating success was partitioned into three categories. The first two categories were randomly selected from an experimental population and included males that: 1) produced EPYs, and 2) had EPFs that did not fledge (EPFs no EPYs). The third category included males without any EP mating success (no EPFs) to serve as a control. To include a variable for local density I counted the number of neighbors for each focal male. Neighbors were defined as warbler pairs with territories adjacent to the focal pair and limited to a radius of three nest-boxes (~160 m) in all directions, which constituted approximately one territory beyond the focal pair.

I monitored all nesting activity of each individual on every study site and recorded the number of warbler offspring produced by each nesting attempt. At the end of each breeding season I had complete information on the identity and reproductive output (warbler offspring fledged) of all warblers breeding on my study sites.

Documenting Site Fidelity and Local Breeding Dispersal

Within each study site I determined the identity of every color-marked individual returning from the previous year and captured and color-marked any individuals that were not banded so that all individuals were color-marked every year. For the purposes of this paper, I focused on the neighborhood fidelity of those males from the “success” treatment group that bred on my experimental study sites in the previous year. I determined whether or not individuals returned to their neighborhoods the following breeding season and searched for any dispersing color-marked birds within a 500-m wide area surrounding each study site. During the years of my study, breeding density on patches did not reach saturation based on the continued increase in population density every year. Maximum box occupancy was ~50% (Chapter 2); therefore, box availability and population densities were unlikely to affect an individual's ability to return to their site

Microsatellite and Paternity Analyses

For more detailed information regarding handling of DNA and methodology for microsatellite protocols and paternity analyses see Chapter 3. In total, on experimental sites, I identified the sire for 99% ($n = 1462$) of all offspring, including both within- and extra-pair. I was able to identify the sire for 92.2% ($n = 116$) of all extra-pair offspring. Average rates of EPFs, and broods and males with at least one EPF are described elsewhere (Chapter 3), but are similar to other territorial, socially monogamous songbirds (Griffith et al. 2002). Overall, I observed a total of 158 successful males ($n = 202$ cases) on experimental study sites from 2002 to 2004.

Statistical Analyses

I used data from all 158 males and 202 cases. Because successful males often returned to the study sites between years, some of them were present for more than one year of the study. Consequently, the descriptive statistics for EP success treatment groups and rates of EPFs are averaged across years. All of these descriptors are reported as the mean \pm 1 SD unless otherwise indicated. I used simple chi-square tests to compare the likelihood of gaining at least one EPF between the two treatment groups of EP success with EPFs.

I used a generalized linear mixed model (GLMM) using GLIMMIX procedures in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) to determine which factors best explained each of the dependent variables. Because some males were present in multiple years I used a repeated measures design by adding a random effect of year for individual males nested within study site to account for non-independence in both models. I evaluated the importance of fixed and random effects using Wald-type statistics reported by the GLIMMIX procedure in SAS. Beginning with a full model that included all fixed and random effects I used a backward stepwise approach by progressively eliminating non-significant fixed effect variables ($\alpha = 0.05$). I added interactions to my models only if there was an a priori prediction. The statistics reported for all non-significant variables are from adding them to the final model.

To examine whether those males with EPYs produced more offspring on average (realized reproductive success) than those with EPFs but no EPYs or those without EPFs I used a GLMM with a Poisson error distribution and a log-link function. The Poisson distribution works best when the response variables are count data (SAS Institute Inc. 2008). Because the total offspring fledged varied by the number of broods

produced, I used the number of broods produced (1 or 2) to offset the model. I included as fixed effects the degree of EP mating success (EPYS, EPFs no EPYs, and no EPFs), whether the male was cuckolded (yes, no) and age [second-year (SY, 1 year old) or after second-year (ASY, 2+ years old)] as categorical variables and the number of successful neighbors (0 to 5) and actual neighbors (1 to 7) as continuous variables. For Poisson GLMMs I used the Kenward-Roger adjustment for calculating the degrees of freedom (Kenward & Roger 1997). The Kenward-Roger adjustment is more robust than SAS defaults methods for small sample sizes and uneven block designs (Kenward & Roger 1997; Kowalchuk et al. 2004).

To determine which factors best explained male neighborhood fidelity I used a GLMM with a binomial error distribution and a logit-link function. I included degree of EP mating success (EPYs, EPFs no EPYs, and no EPFs), male cuckolded (yes, no), age (1 year old, 2+ years old), and broods fledged (1 or 2) as categorical fixed effects and the number of successful neighbors (0 to 5) was included as a continuous variable. I used the Laplace approximation method for approximating the likelihood because the penalized quasi-likelihood (PQL) method, the default in SAS, can be biased for binary data (Bolker et al. 2009). All values presented from model estimates are means \pm 1 SE unless otherwise indicated.

Results

Rates of Extra-Pair Matings

From 2002 to 2004 on experimental sites, the population-wide (successful plus unsuccessful males) average proportion of broods and males with at least one extra-pair fertilization across years was $20.5 \pm 5.0\%$ (mean \pm SD) ($n = 409$) and $18.8 \pm 3.0\%$ (mean \pm SD) ($n = 306$), respectively. Focal males that successfully gained

EPFs sired on average 1.58 ± 1.14 (mean \pm SD, $n = 45$, range = 1 to 7) EP nestlings and there was no difference in the total number of EPFs between males that did and did not gain EPYs [EPYs: 1.73 ± 0.269 , mean \pm SE ($n = 28$ cases); EPFs no EPYs: 1.41 ± 0.173 ($n = 17$ cases) t-test; $t_{43} = -0.881$, $p = 0.383$]. On average, $63.4 \pm 3.3\%$ ($n = 45$) of males with EPFs had at least one of their offspring successfully fledge from a neighbor's nest. Males with EPYs ($n = 28$) fledged an average of 1.68 ± 1.34 (mean \pm SD) EP offspring via successful neighbor pairs.

Focal Males

A total of 158 different successful males ($n = 202$ cases) were included as focal males in the experiment. Each male was present an average of 1.34 ± 0.59 (mean \pm SD) years during the three-year study period. Of this total of focal males, $72.1 \pm 12.7\%$ and $27.9 \pm 12.7\%$ produced one or two broods, respectively. The average number of successful and actual neighbors was 2.3 ± 0.26 (mean \pm SD, range = 0 to 5) and 3.2 ± 0.46 (range = 1 to 6), respectively.

The realized reproductive success of males with EPYs was significantly higher than both those without EPFs and those with EPFs but no EPYs after controlling for broods and taking into account the number of offspring fledged from their own nests, those lost to cuckoldry, and those gained via EP mating (Table 5-1, Figure 5-1).

Site and Neighborhood Fidelity

Averages of $60.6 \pm 7.4\%$ and $50.9 \pm 11.3\%$ of focal males returned between years to their patch and neighborhood, respectively. The EP category predicted the neighborhood fidelity of all males regardless of the number of broods fledged, whether or not the male was cuckolded, the number of successful neighbors, and age (Table 5-2, Figure 5-3). Neighborhood fidelity of males gaining EPYs was nearly twice

that for males without EPYs (Figure 5-3). The neighborhood fidelity of those groups of males that did not gain any EPYs, either because they did not gain EPFs or because their EPFs did not result in fledged offspring, did not differ from each other [No EPFs, 48% (n= 157 cases), EPFs no EPYs, 42% (n=17 cases): $X^2_1 = 0.353$, $p = 0.616$].

Discussion

I experimentally examined whether the realized reproductive success of male prothonotary warblers was increased by the fledging of EP offspring and whether males were aware of this EP mating success based on their breeding dispersal decisions. My experiment significantly increased male realized reproductive success by experimentally fledging EP offspring of some males but not others, which subsequently influenced male neighborhood fidelity. Males that had EPYs with a neighbor produced two more offspring on average per year and returned to their neighborhood in the subsequent year at nearly twice the rate of those males with EPFs that failed to fledge and males without EPFs. To my knowledge, this is the first study to demonstrate that males are aware of their own EPYs. Because males were blindly selected to gain EPYs by manipulating the success of neighbors, I eliminated the potential confound of male quality on return rates and showed that males are able to assess their own EP mating success.

I believe that this awareness of EPYs requires a two-step process where males copulate with a particular EP female and then the same female subsequently fledges the brood of offspring. It is possible that males in the other two EP mating success categories could be responding in a similar way such that males with EP copulations (without fertilizations) with a successful neighbor could be returning to their neighborhoods at a similarly high rate. If I assume EP copulation rates are correlated

with EP fertilization rates, then I should have seen an increased and likely intermediate response from those males with EPFs but no EPYs, which I did not. Although I acknowledge that copulation rates are difficult to quantify, I feel that my assumption that male EP copulation rates are correlated with EP fertilization rates is warranted given that other studies have shown that observed copulation rates are relatively infrequent and are correlated with fertilization rates (Michl et al. 2002; Townsend 2009) even in species with higher rates of EP offspring than my study population. Therefore, I conclude that EP copulations in my system are relatively rare and have a high predictive power in determining EP success, although I cannot rule out alternatives such as the possibility of kin recognition.

Kin recognition in socially monogamous birds is thought to be rare even though promiscuity is widespread (Kempnaers & Sheldon 1996), but may be more common in social systems where interactions with kin are more common (e.g., cooperative and colonial breeders). In several studies, the experimental reduction of a male's ability to mate guard and copulate with his mate, which was to represent infidelity of their mate, was sufficient to reduce male parental care (Moller 1988; Davies et al. 1992; Sheldon & Ellegren 1998) and nestling defense (Moller 1991). Sheldon & Ellegren (1998) controlled for direct cues from kin recognition by cross-fostering broods in their experiment and showed that males were just as likely to reduce parental care with a reduction of their share of paternity without regard to how many of his own offspring were actually present. This suggests that a male's perception of paternity can be altered by preventing him from mate guarding and copulating with his mate during part of her fertile period and is unlikely to arise due to kin recognition. Similar recognition of EP

mating success could result from increased copulations with particular EP females provided that the frequency of copulations and fertilizations are highly matched.

Extra-pair copulations may be a less reliable indication of paternity, however, in species where EP offspring typically outnumber within-pair offspring (Griffith et al. 2002; Griffith 2007), females cryptically choose sires during the post-copulation period (Birkhead & Møller 1998; Pizzari et al. 2002), and/or copulations are used as a coercive tool to manipulate helping or parental care (Parish & De Waal 2000; Rubenstein 2007).

Males may increase their fitness via gaining EPYs, which is not possible for females in my system. In fact, on average, males produced more offspring if they gained EPYs even after taking into account losses in paternity. Fitness benefits of extra-pair versus within-pair offspring are unknown in my system and estimates of these benefits are necessary to assess the true fitness value of EP offspring. Moreover, if males are aware of their EP mating success, then it might also be possible for them to assess infidelity of their own mate. Future research is needed to address whether cuckolded males are aware of losses in paternity and subsequently withhold parental care, which would support the idea of indirect selection on female promiscuity (Arnqvist & Kirkpatrick 2005). Although still widely debated, it is thought that females control EP mating opportunities (Double & Cockburn 2000; Eliassen & Kokko 2008). If this is true, then there may be strong selection on males to exert control of female infidelity through reducing parental care or exploit infidelity by returning to locations with verified EP mating success.

Table 5-1. Results of GLMM (Poisson error and log link function) on the total number of offspring fledged (accounting for cuckoldry and EP fledging success) by male prothonotary warblers ($n = 158$; $n = 202$ cases) in relation to EP mating success, neighbor success and age. Model is offset by the number of broods fledged (1, 2) in the season from their own nest. Estimates for the repeated measures random effect* of individual (patch) by year is from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
EP mating success	$X^2_{2,38} = 21.51$		< 0.001
No EPFs		-0.369 \pm 0.081	
EPFs no EPYs		-0.369 \pm 0.127	
EPYs		0	
Male cuckolded	$X^2_{1,38} = 12.92$		<0.001
No		0.274 \pm 0.076	
Yes		0	
Removed variables			
Number of neighbors (0 to 6)	$X^2_{1,37} = 1.93$	0.037 \pm 0.027	0.164
Successful neighbors (0 to 5)	$X^2_{1,37} = 1.88$	0.038 \pm 0.028	0.171
Age 1 year old	$X^2_{1,37} = 1.67$	-0.092 \pm 0.072	0.197
2+ years old		0	
Individual (patch) by year*	-----	0	-----

^a Estimates are on a log scale. Estimates of removed variables are from when they were added alone to the final model.

Table 5-2. Results of GLMM (binomial error and logit link function) on the probability of between-year neighborhood fidelity of male prothonotary warblers ($n = 158$ males, $n = 202$ cases) in relation to public and private information. Fixed effects in bold were retained in the final model. Estimates for the repeated measures random effect* of individual (patch) by year is from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
EP mating success	$X^2_{2, 38} = 11.64$		0.003
No EPFs		-1.983 \pm 0.562	0.002
EPFs no EPYs		-2.261 \pm 0.791	0.007
EPYs		0	
Individual (patch) by year*	$Z = 0.58$	0.279 \pm 0.481	0.281
Removed variables			
Male cuckolded	$X^2_{1, 37} = 0.59$		
No		-0.287 \pm 0.375	0.444
Yes		0	
Broods	$X^2_{1, 37} = 0.40$		
1		-0.223 \pm 0.352	0.526
2		0	
Successful neighbors (0 to 5)	$X^2_{1, 37} = 0.06$	0.033 \pm 0.139	0.811
Age 1 year old	$X^2_{1, 37} = 0.02$	-0.043 \pm 0.301	0.889
2+ years old		0	

^a Estimates are on a logit scale. Estimates of removed variables are from when they were added alone to the final model.

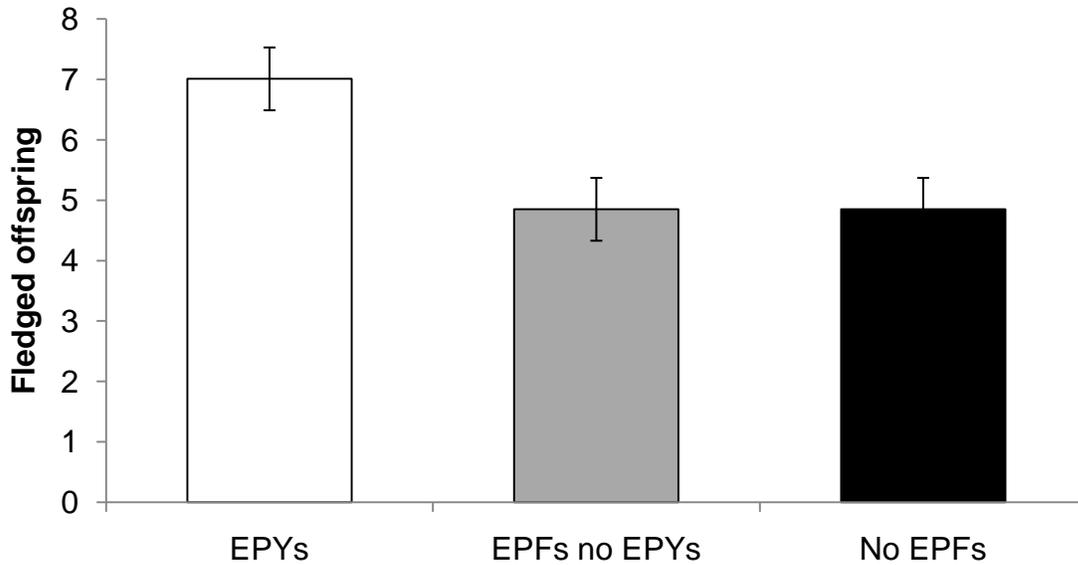


Figure 5-1. Estimates of mean \pm SE realized reproductive success (number of fledged warbler offspring) per male per year in relation to the fledging of extra-pair offspring. Realized reproductive success takes into account the offspring fledged from their own nest minus those lost to cuckolding plus any EPYs (see Appendix Figure A-9 for actual mean \pm SE number of offspring fledged by group)

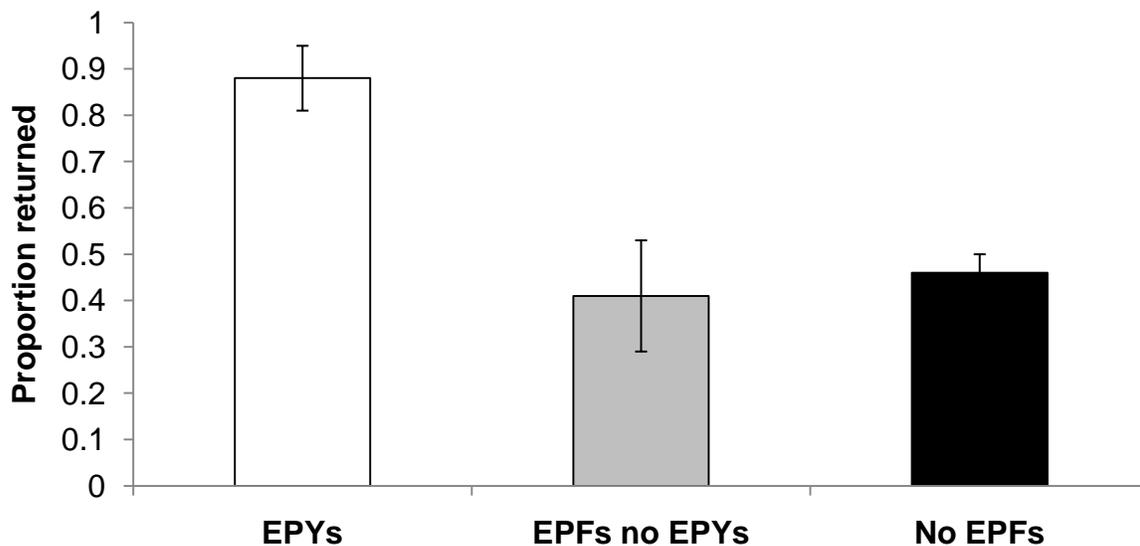


Figure 5-2. Estimates of mean \pm SE rates of neighborhood fidelity of breeding males in relation to degree of EP mating success in the previous year. Male assignment to the EPFs no EPYs and EPYs groups was due directly to an experimental manipulation of neighbor success (see Appendix Figure A-10 for actual proportion of males that returned to their neighborhoods between years)

CHAPTER 6
BENEFITS OF SITE FAMILIARITY: MALE SITE-SPECIFIC BREEDING EXPERIENCE
AND NOT AGE PREDICTS EXTRA-PAIR MATING SUCCESS IN A WILD BIRD
POPULATION

Introduction

Individuals make dispersal decisions that can lead to significant variation in lifetime reproductive success and ultimately result in the evolution of species- and/or higher order taxon-wide dispersal patterns (Clobert et al. 2009; Hawkes 2009). Although natal dispersal is typically more extensive (Clobert et al. 2001), breeding dispersal can occur repeatedly throughout an individual's lifetime and therefore have large effects on individual fitness. Sex-biased breeding dispersal is a common pattern in animal systems (Greenwood 1980; Greenwood & Harvey 1982). Female-biased breeding dispersal in the majority of avian species has long been thought to result from the prevailing mating system placing gender-specific selective pressures on individuals, leading to asymmetrical benefits of site familiarity to territorial males and inbreeding avoidance in females (Greenwood 1980; Greenwood & Harvey 1982; Clobert et al. 2001; Gros et al. 2008).

Empirical evidence of asymmetrical benefits of site or territory familiarity in breeding male birds has been limited to quantifying the advantages in territory defense, both in their ability to defend it (Krebs 1982; Beletsky & Orians 1989a) and/or the reduced energetic costs associated with having familiar neighbors (Fisher 1954; Temeles 1994; Akçay et al. 2009) (but also see Lampe & Slagsvold 1998 for potential female benefit of familiar neighbors). Although advantages of territory defense are likely to contribute positively to a male's reproductive success or fitness, it does not explain why males are more likely to remain and defend poor quality territories (e.g., those with

high nest predation) whereas females seem to respond adaptively and disperse (Greenwood & Harvey 1982; Payne & Payne 1993; Haas 1998; Hoover 2003a). In fact, measureable fitness benefits to males that return to familiar areas, that do not similarly affect females, is generally lacking (but see Beletsky & Orians 1989b; Piper et al. 2008).

Breeding males that move to unfamiliar areas may suffer costs of reduced reproductive success for two reasons: 1) they do not know, in advance, which areas will be more productive (due to nest predation) unless they have had a chance to prospect in new areas and 2) they may be less competitive amongst unfamiliar neighbors and be relegated to less preferred territories (Petit & Petit 1996), which could mean lower extra-pair (EP) mating success, and/or increased risk of cuckoldry. If reduced reproductive success results from dispersal to new sites, then males should be reluctant to leave a familiar area unless reproductive prospects on their current site are dismal at best (e. g., because of nest predation and/or few females on the site).

Males, but not females, in many socially monogamous birds can numerically increase their number of offspring via extra-pair mating opportunities (Griffith et al. 2002). Although EP mating is evolutionarily important to females, presumably by improving offspring quality, females are limited in their ability to increase offspring number because of sexual asymmetries in gamete investment and parental care (Bateman 1948; Trivers 1982). Hence, dispersal decisions of males and females likely vary according to the respective fitness costs and benefits for each sex. A relatively widespread pattern amongst territorial songbirds is that dispersal propensity tends to decline with age, particularly in males (Greenwood & Harvey 1982). Another emerging pattern is that older males tend to have higher EP mating success (Akçay &

Roughgarden 2007; Bouwman et al. 2007; Schmoll et al. 2007). Typically, authors suggest that male age is correlated with “good genes” (but see Akcay & Roughgarden 2007 and references therein), however, age and thus EP mating success is potentially correlated with prior breeding experience (Weatherhead & Boag 1995) or site familiarity.

In this study, I examined whether males familiar with a breeding patch as a result of prior breeding experience enhanced their future mating prospects in the form of EP fertilizations. Specifically I tested whether prior EP mating and breeding experience (no breeding experience on site, bred on site without EPFs, bred on site with EPFs) on a site in year $x-1$, and/or the number of neighbors influenced the probability that a male gained EPFs in year x . Prior experimental research in my system on prothonotary warblers (*Protonotaria citrea*) revealed that males, even when unsuccessful on a territory, were more likely to return to their familiar neighborhood between years than females (Chapters 2 & 3). I also showed experimentally that those males that successfully fledged EP offspring with neighbors were more than twice as likely to return to their neighborhoods in the subsequent year as males lacking EP offspring (91 vs. 42%) (Chapters 3 & 5). Additionally, the probability of males returning to their neighborhoods increased with the number of successful neighbors (Chapters 2 & 3), most likely because this was correlated with EP fledging success (Chapter 3). The evolution of such dispersal decision rules typically requires that the information used is relatively predictable between years so that information in one year adequately predicts productivity in the next (Switzer 1993; Doligez et al. 2003). Because both males and females successful in their own nesting attempts return at a rate of ~70%/year (Hoover 2003a), the number of successful neighbors in one year leads to a predictably high

probability of having more familiar neighbors in the next. Although still widely debated, it is thought that females control EP mating opportunities (Double & Cockburn 2000; Eliassen & Kokko 2008). Also, sexual selection theory assumes that female mate preferences for particular male phenotypes are heritable and repeatable (Lande 1981; Kirkpatrick 1982). If these premises are true, then there may be strong selection on males to exert the only control they have on producing EP offspring, which is by returning to familiar areas with predictably more EP mating opportunity and where they know they were previously competitive or preferred by neighboring females amongst neighboring males.

I have previously manipulated individual reproductive success (IRS) by randomly controlling nest predation of prothonotary warbler pairs (Hoover 2003a). Subsequent male dispersal decisions were based on an experimental assignment of IRS, neighborhood success, and EP fledging success and less likely to be associated with male quality (Chapters 3 & 5). In this study, I used data from the returning and newly immigrating males on my experimental sites and examined the effects of prior male breeding experience or familiarity with a site on future male EP mating success. I also wanted to contrast experience with age to determine whether one variable better explained extra-pair fertilization (EPF) success. By using the known-age portion of my population I examined whether the actual age (1 to 7 years) of males and/or breeding experience significantly increased EPF success. Specifically, I determined whether the level of prior breeding experience and success with EPFs (no breeding experience on site regardless of age, bred on site without gaining EPFs, bred on site and gained

EPFs) and/or neighborhood size in the current year, rather than male age best predicted future male EPF success.

I also tested whether informed dispersal based on previous breeding experience on the site, or age could explain differences in first clutch dates and neighborhood size in an attempt to disentangle the influence of site familiarity and age on when and where males breed. Because male warblers returned to their neighborhood at such high rates based on the fledging of EP offspring and neighborhood success (Chapters 3 & 5), and older males generally return to the breeding grounds prior to younger males, I predicted that prior breeding experience would give male's an advantage in selecting territories in areas where larger neighborhoods would form and where they would be successful at gaining EPFs again. I further examined whether prior breeding experience or age influenced cuckoldry rates to determine whether or not males with EP mating success had a net reproductive advantage. I predicted that male age and breeding experience would have little explanatory power for female infidelity given that past research showed that females tended to cuckold their social mates as a potential inbreeding avoidance mechanism (Chapter 4). This is the first study, to my knowledge, to contrast the effects of prior breeding experience and age on the EP mating success of males.

Methods

Study Area and Study Organism

I conducted this research within the Cache River Watershed in Illinois, USA (37° 18' N, 88° 58' W). I chose four study sites from a network of 16, each containing at least eight pairs of warblers that were in discrete patches of forested wetland habitat. I focused on discrete patches where I could monitor and genetically sample all offspring and to minimize potential adjacent areas where males could seek additional EP

fertilizations. These four study sites were separated from each other by at least one kilometer of habitat not suitable for breeding prothonotary warblers (e.g., upland forests, agriculture, or successional habitat) and ranged in size from 10 to 44 ha.

The prothonotary warbler is a migratory songbird that winters in the Neotropics and breeds in the central and eastern United States (Petit 1999). This species is territorial and socially monogamous (Petit & Petit 1996), nests in secondary cavities, and associates closely with standing water in bottomland and swamp forests (Petit 1999). Prothonotary warblers prefer to nest over water (Petit and Petit 1996) and readily use nest boxes when available (Hoover 2003a; Petit 1989; Blem & Blem 1994). Additional details of its natural history and behavior are given elsewhere (Petit 1999; Hoover 2003b, 2006).

Monitoring Individuals and Manipulating Nesting Success

During 2002 to 2004 I monitored breeding populations of prothonotary warblers using nest boxes. Methodology for nest box placement, attachment, and spatial arrangement are described elsewhere (Chapter 2 & 3) (see Hoover 2003a for additional details of nest boxes and nest monitoring protocol).

I captured or re-sighted all individual warblers on all study sites every year and color-marked each male and female with a unique combination of a numbered aluminum and colored plastic leg bands. I measured and recorded wing chord (mm), tarsus (mm), tail length (mm) and mass (g) for all adults captured. I collected ~10- μ l blood samples from all adults and nestlings on the chosen study sites by brachial puncture using a 26G1/2 needle (BD-Becton-Dickinson) and micro-hematocrit tubes (Fisher Scientific, Pittsburgh, PA, USA). I stored all blood samples in Queen's lysis buffer (Seutin et al. 1991) at room temperature while in the field and later stored all

blood samples at -20°C . Males were captured at least once in mist nets by placing a decoy of a male warbler in front of a mist net within the territory of the male while playing a recording of a male prothonotary warbler song. Males became resistant to being captured over time so I did not catch all males every year. I captured all females by placing a small plastic bag over the openings of nest boxes while they were incubating eggs. I knew the identity of the male and female associated with every nesting attempt each year on my study sites. Adults were aged as either second-year (SY: 1 year old) or after second-year (ASY: 2+ years old) based on plumage (Pyle 2001) and morphometric characteristics of known-age birds (unpublished data J. Hoover). Known-ages were based on either recruited juveniles individually banded in my study system, or males identified initially as SY birds.

During each year from 2002 to 2004 I experimentally manipulated the nesting success of individual pairs on each of the four study sites so that approximately one-third of pairs “failed” each year (similar to natural levels of reproductive output Hoover 2001 in another study). The remaining pairs were assigned the “success” treatment and all nest boxes were protected from raccoons (*Procyon lotor*), the main nest predator in the system (Hoover 2003a, 2006). I removed nest boxes from trees and reattached them to two pieces of 1.50-cm-diameter greased conduit placed in the ground and standing one meter away from the original nest tree. Nest boxes on conduit were safe from nest predation so that I could control when predation occurred and take blood samples from all of the nestlings.

I then manipulated all nesting attempts of pairs from the “failure” treatment to simulate nest predation and prevent them from fledging any nestlings. For each nesting

attempt of the unsuccessful pairs I removed nestlings when they were 4 to 6 days old (they fledge on day 11) and pulled some of the nesting material into the opening of the nest box to mimic nest predation by a raccoon. I relocated these nestlings to the nests of foster parents on other sites not included in the experiment. As a result of my manipulations, I experimentally influenced male neighborhood fidelity in year x by randomly manipulating neighborhood success and the fledging or not of extra-pair offspring in year $x-1$ (Chapters 3 & 5). Male presence (present or not) and EP mating (EPFs or not) in any year, however, were not experimentally controlled. Neighbors were defined as warbler pairs with territories adjacent to the focal pair and limited to a radius of three nest-boxes (~160 m) in all directions, which constituted approximately one territory deep surrounding the focal pair.

I monitored all nesting activity of each individual on every study site, recorded the number of warbler offspring produced by each nesting attempt, and therefore had complete information on the identity and reproductive output (warbler offspring fledged) of all warblers at the end of each breeding season.

Documenting Site Fidelity and Local Breeding Dispersal

Within each study site I determined the identity of every color-marked individual returning from the previous year and captured and color-marked any new individuals so that all individuals were color-marked every year. For the purposes of this paper, I assumed the level of a male's experience on a site was based on being captured or seen on a given site and whether they sired any of the sampled EP offspring. In a few cases ($n = 4$) males returned to breed in year x that had been genetically detected as sires of EP offspring but not recorded as breeding in a nest box in year $x-1$. Because I

did not know if these males had been floaters or made a nesting attempt that failed too quickly to be detected, I omitted them from any analyses.

Microsatellite and Paternity Analyses

For more detailed information regarding handling of DNA and methodology for microsatellite protocols, paternity analyses see Chapter 3. In total, on experimental sites, I identified the sire for 99% ($n = 1462$) of all offspring, including within- and extra-pair, on experimental sites. I was able to identify the sire for 92.2% ($n = 116$) of all extra-pair offspring. Average rates of EP offspring, and broods and males with at least one EP offspring are described elsewhere (Chapter 3).

Statistical Analyses

I used data from a total of 200 different males and 294 cases. Because the nature of my question required that some males returned to the study sites between years, some of them were present for more than one year of the study. Consequently, the descriptive statistics for rates of extra-pair offspring and neighborhood size were presented as the average across years. All of these descriptors are reported as the mean \pm 1 SD unless otherwise indicated. I used simple chi-square tests to compare the likelihood of gaining at least one EPF and ANOVA to compare the number of offspring sired by males with EPFs between years.

In general, I used generalized linear mixed (GLMM) or general linear mixed (GLM) models using GLIMMIX and MIXED procedures in SAS 9.2 (SAS Institute, Inc., Cary, NC, USA) to determine which factors best explained each of the dependent variables. Continuous dependent variables were examined for normality prior to selecting the appropriate model. Because I had many individuals return to my study sites between years I always used a repeated measures design by adding a random effect of year by

individual males nested within study site to account for non-independence of cases in all models. I evaluated the importance of fixed effects using Wald-type statistics and F-statistics reported by the GLIMMIX and MIXED procedures respectively in SAS and used the ratio of the chi-squared statistic to degrees of freedom to evaluate evidence of over-dispersion ($\hat{c} < 1.2$). Beginning with a full model that included all *a priori* fixed and random effects I used a backward stepwise approach by progressively eliminating non-significant fixed effect variables ($\alpha=0.05$). I added interactions to my models only if there was an *a priori* prediction that an interaction may be important. The statistics reported for all non-significant variables are from when they are added back into the final model.

To examine whether the previous breeding experience, number of neighbors and/or age category significantly influenced the probability that a male would gain at least one EPF in year x I used a GLMM with a binomial error distribution (response variable coded as “0” and “1”) and a logit-link function. I included number of neighbors (0 to 6) in year x as a scale variable, previous breeding experience in year $x-1$ (no breeding experience on site, bred on site without EPFs, bred on site with EPFs), and age (1, 2+ years old) in year x as categorical fixed effects. For all GLMMs using a binomial distribution I used the Laplace approximation method for approximating the likelihood because the penalized quasi-likelihood (PQL) method, the default in SAS, can be biased for binary data (Bolker et al. 2009). To determine if, in a known-age sub-sample of males ($n = 152$ males; $n = 218$ cases), actual age increased a males probability of gaining at least one EPF I re-ran the model above replacing age category with known-age (1 to 7 years old). I combined all males with any prior breeding

experience regarding EPF status in year $x-1$ into a single category and used the binomial variable prior breeding experience (no or yes) and removed number of neighbors in this analysis due to smaller sample sizes.

To examine whether breeding experience or age category influenced breeding date of males I used a GLM with individual (site)-by-year as a random effect. I included intercept in the final model and used Julian day (e.g., 10 May = 130) of a male's first clutch date as the continuous dependent variable and previous breeding experience in year $x-1$ (no breeding experience on site, bred on site without EPFs, bred on site with EPFs), year (2002 to 2004), age (1, 2+ years old) in year x , and the interaction between age and experience as categorical fixed effects. I included year in this model because previous data suggest that individuals can track inter-annual variation in early spring temperatures by adjusting their first clutch dates during warmer or colder years (J. Hoover unpublished data).

To determine which factor most influenced how many neighbors a male had I constructed a GLM as described above. In this case I used number of neighbors as the dependent variable and previous breeding experience in year $x-1$ (no breeding experience on site, bred on site without EPFs, bred on site with EPFs), age (1, 2+ years) in year x as categorical fixed effects and Julian day of first clutch date as a continuous fixed effect.

To determine if males were more or less likely to lose paternity in their own nest I used a GLMM with a Poisson error distribution and a log-link function using the number of offspring lost to cuckoldry as the response variable. The Poisson distribution works best when the response variables are count data that are not normally distributed (SAS

Institute Inc. 2008). Because the probability of losing any offspring to cuckoldry increased with the number of offspring sampled I included this continuous variable in the model. I also included previous breeding experience in year $x-1$ (no breeding experience on site, bred on site without EPFs, bred on site with EPFs), and age category (1, 2+ years) in year x as categorical fixed effects. For a GLMM using a Poisson error distribution I used the Kenward-Roger adjustment for calculating the degrees of freedom (Kenward & Roger 1997). The Kenward-Roger adjustment is more robust than SAS defaults methods for small sample sizes and uneven block designs (Kenward & Roger 1997; Kowalchuk et al. 2004).

Results

A total of 200 different males ($n = 294$ cases) were included in the study. Each male was present an average of 1.47 ± 0.69 (mean \pm SD) years during the three-year study period and had on average 3.02 ± 1.25 neighbors (mean \pm SD, range: 0 to 6). Males that successfully gained EPFs sired an average of 1.65 ± 0.87 (mean \pm SD, $n = 41$, range = 1 to 7) EP offspring each year. There was no difference in the proportion of males gaining at least one EPF (Chi-square: $X^2_2 = 1.79$, $p = 0.409$) nor the average number of extra-pair offspring sired by extra-pair males (ANOVA: $F_{2,50} = 0.04$, $p = 0.96$) among years.

Male Extra-Pair Fertilization Success

The probability a male sired at least one EP offspring in year x depended on both the number of neighbors in year x and the level of breeding experience on the site in the previous year ($x-1$) (Table 6-1, Figure 6-1). Regardless of age (1 versus 2+ years old) and previous success in gaining EPFs in year $x-1$, experienced males had a higher probability of siring at least one EPY in year x than those males without prior breeding

experience on the site (Figure 6-2). The probability males sired any EP offspring in year x , regardless of breeding experience in year $x-1$, also increased with an increase in the number of neighbors in year x (Figure 6-1). If the probability of siring EP offspring was a function of mate choice preferences of the same females, then I would predict that the majority of cases where males that successfully sired EP offspring in two consecutive years would either be with the same female or a result of cuckolding the same inferior male. The minority of cases were explained by repeated mating events with the same neighbors. Of those males that gained EPFs two years in row ($n = 12$), only 8.3% were with the same female and only 25% resulted from cuckolding the same male.

Known-Age Males and Extra-Pair Mating Success

To examine whether there was an increase in EPF probability with actual age I used a smaller data set consisting of 152 males ($n = 218$ cases) of known ages (1 to 7 years). Because the males with some on-site breeding experience in year $x-1$, regardless of gaining EPFs, did not differ in their probability of siring at least one EP offspring in year x , I combined them for comparison to those with no experience in year $x-1$. Actual age in year x did not influence EP mating success in year x when controlling for breeding experience in year $x-1$ (GLMM, $\beta \pm SE = -0.116 \pm 0.262$, $X^2_{1, 77} = 0.02$, $p = 0.657$) (Figure 6-3). By removing the effect of known-age from the model, 15.9 ± 4.4 % of males with breeding experience in year $x-1$ sired at least one EP offspring in year x versus only 1.9 ± 0.74 % of males with no prior breeding experience on the site in the previous year (GLMM, $\beta \pm SE = -2.28 \pm 0.483$, $X^2_{1, 78} = 22.22$, $p < 0.0001$). To examine whether experienced individuals were larger (i.e., higher quality) I compared male condition (std. residuals of mass x tarsus regression) of all males two years old or older. I found no difference or tendency in the relative condition

in year x of those that did and did not have previous breeding experience on the site (t-test: $t_{24} = 0.25$, $p = 0.980$).

Breeding Phenology and Neighborhood Size

The average first clutch date for all males differed between years (REML: $F_{2, 169} = 10.12$, $p < 0.0001$) with 2002 [Julian day = 149 ± 1.9 (29 May)] being eleven days later than 2004 [138 ± 1.4 (18 May)] ($p < 0.0001$); whereas, 2003 [Julian day = 143 ± 1.8 (23 May)] was intermediate and did not differ from either year (vs. 2002: $p = 0.054$; 2004: $p = 0.162$). Male age (1 year old, 2+ years old) in year x significantly influenced first clutch dates in year x with older males breeding an average of nine days earlier (Julian day = 139 ± 1.2) than young males (Julian day = 148 ± 1.5) (REML: $F_{1, 237} = 20.39$, $p < 0.0001$). Level of breeding experience in year $x-1$, did not, however, influence first clutch dates in year x (linear mixed model: $F_{2, 206} = 0.760$, $p = 0.469$).

Only level of breeding experience on the site in the previous year and date of first clutch in year x , but not age in year x , influenced the size of a male's neighborhood. Males with prior breeding experience on the site with EPFs in year $x-1$ were in the largest neighborhoods in year x and those without any breeding experience on the site in year $x-1$ had the fewest neighbors in year x after controlling for date of first clutch (Table 6-2, Figure 6-4). Males that generally started breeding later in the season ended up with fewer neighbors (Table 6-2).

Offspring Lost to Cuckoldry

The only factor associated with the number of offspring lost to cuckoldry in year x was the total number of offspring sampled in that year. As expected, my ability to detect cuckolded offspring increased with the number offspring I sampled for a given male (Table 6-3). There was no association of males losing paternity in their own broods,

however, with breeding experience in year *x-1*, age category (1 year old, 2+ years old), actual neighbors, male infidelity (EPF no or yes), or male condition. The random effect of site (individual) by year was significant such that the number of offspring lost to cuckoldry was associated with some individual males and not others (Table 6-3).

Discussion

The results of this study show clearly that prior experience, and not age or previous history of gaining EPFs provides the chief benefit of site fidelity in males. This is the first study to experimentally tease apart effects of age and prior residence (but see Perreault et al. 1997), which are correlated in most study systems (Weatherhead & Boag 1995; Kleven et al. 2006; Akçay & Roughgarden 2007; Bouwman et al. 2007; Schmoll et al. 2007). Male prothonotary warblers with any form of prior breeding experience on a site were more likely to gain EPFs compared to those males of similar ages without site familiarity. Thus, it is not male age, per se, that seems to affect female choices to participate in EP mating. Males with site familiarity ended up in larger neighborhoods with access to more females whereas females seemed to use EP mating to increase genetic compatibility when their social mate was closely related (Chapter 4). My results therefore support Akçay & Roughgarden (2007) whom suggested that alternative mechanisms could be creating the pattern of age and EP mating. They appropriately dismissed the circular argument for age being correlated with “good genes” because the majority of evidence comes from the extra-pair literature (Brooks & Kemp 2001) and relies on accepting the “good genes” hypothesis as the main cause of extra-pair. Unlike the males, females in my system cannot increase reproductive success outside of their own nesting attempts given that I found no evidence of conspecific brood parasitism (Chapter 3). Females dispersed farther,

between-years, than males (Chapter 2), with the longest dispersal distances being of those females closely related to their social mate (Chapter 4). Hence, cuckoldry or EP mating has directly opposite effects on male and female dispersal decisions.

Experience, Age, and Good Neighborhoods

Age and not experience best explained the first clutch dates of all males, however, experienced males ended up breeding in larger neighborhoods. Although experience on the site did not give males an advantage when it came to maintaining paternity of their own offspring as a result of cuckoldry, neither did age, neighborhood density, male condition, nor male infidelity. Males on familiar sites and in larger neighborhoods gained more EPFs but were not more or less likely to lose offspring to cuckoldry, which, for those males, resulted in a net reproductive gain relative to males dispersing to unfamiliar patches. Because older males start breeding earlier than younger males, they require previous knowledge of patch social dynamics and territory quality to make informed decisions about where to settle and start breeding. Only if older males settling early have prior breeding experience on a site do they know in advance where larger neighborhoods will form. The use of public information or the reproductive performance of conspecifics collected by dispersing birds in the previous year (Danchin et al. 2001; Doligez et al. 2002) can improve dispersal decisions on a coarse scale (good versus bad), however, actual breeding experience on the site seems to contribute to better discrimination of territory quality and EP mating opportunity.

In addition to the benefits of breeding in larger neighborhoods, experienced males were more likely to gain EPFs than inexperienced males in similarly sized neighborhoods, suggesting that familiarity with their territory, site, or neighbors influence their EP mating success. Although female preferences are expected to be heritable and

repeatable (Lande 1981; Kirkpatrick 1982) only 8% of males that gained EPFs in two consecutive years did do so with the same female. In my system, this result is not too surprising given that females tend to disperse between years if they cuckolded their mate (i.e., high relatedness to social mate, Chapter 4). Only 25% of the cases of males repeatedly gaining EPFs across years involved cuckolding the same male. Gaining EP for a particular male rarely involved the same neighbors, which suggests that familiarity with neighboring males and/or females is not the primary reason for repeated EP mating success. A closer examination of males and their familiarity with neighbors, territories, or social mates will be necessary to understand exactly why males with breeding experience on a site have an EP mating advantage.

Male Quality and Site Familiarity

Although there is some evidence that low quality prothonotary warbler males end up in poorer quality habitat given their inability to defeat a dominant male on a preferred territory (Petit & Petit 1996), prior breeding experience and/or tenure duration can significantly alter a male's tenacity and willingness to defend a familiar, high quality area (Krebs 1982; Beletsky & Orians 1989a). Several lines of evidence suggest that, in my study, males familiar with their site (and hence more likely to gain EPFs) were not necessarily of higher quality. First, previous research has documented that prothonotary warbler movements between sites are an adaptive response to reproductive failure resulting from nest predation and not a function of individual quality (Hoover 2003a). Second, my experimental design was likely the best way to control or limit the potential confound of male quality. For males breeding on my sites, I experimentally manipulated success or failure in their own nest, the number of successful neighbors, and whether or not they fledged EP offspring, which subsequently influenced their decision to return to

their neighborhoods. Third, if males with prior experience on a site were of better quality than inexperienced males, then I would expect those with experience to either arrive or be chosen by a female sooner and thus be paired and breeding earlier. Experienced males, however, did not start breeding significantly sooner than similarly-aged inexperienced males. In fact, like the majority of migratory songbirds (Gill 1995), age and not experience was the best predictor of breeding date after controlling for inter-annual effects on first clutch dates. Fourth, many of the males went from having no EPFs in one year to gaining them in the next. This was true of both the inexperienced males and males with prior breeding experience on the site that had failed to gain EPFs. In addition, inexperienced males that did ($n = 10$) and did not ($n = 80$) gain EPFs in their first year on a site had nearly identical rates of EPFs when they returned to the site the following year [30% and 28.8%, respectively; Chi-square (exact): $X^2_1 = 0.007$, $p = 0.934$]. Lastly, if males that gained EPFs were of better quality than those that did not, I would predict that the likelihood of cuckoldry would differ between the two groups of males. To the contrary, males that gained EPFs were just as likely to lose some offspring in their own nest to cuckoldry as males that failed to gain EPFs. Collectively, these lines of evidence strongly suggest that site familiarity, rather than male quality, is the primary factor affecting male success in gaining EPFs.

Site Familiarity and the Extra-Pair Advantage

Why do males with prior breeding experience on the site garner an EPF advantage? It may be that because experienced males end up in larger neighborhoods and start breeding early they have an advantage due to asynchrony of neighboring nests; however, comparisons among different migratory passerines suggest that breeding synchrony and not asynchrony increases rates of EPFs (Albrecht et al. 2007).

Within species, earlier breeders could have an advantage if they have enough EP mating opportunities as was shown experimentally by Vaclav & Hoi (2007) in house sparrows (*Passer domesticus*), who found that birds that laid eggs earlier relative to their neighbors increased EP mating success. Hence, only males in larger neighborhoods that start breeding earlier as a result of prior breeding experience should disproportionately improve their chances of EP mating success. A careful examination of clutch dates in neighborhoods will be necessary to determine if laying order can explain the advantage of previous breeding experience. This explanation seems plausible given that males having bred on the site either with or without EPFs in year $x-1$ had a relatively equal probability of gaining EPFs in year x .

One other possibility that could explain the familiarity advantage is that because males likely know some of their male neighbors due to habitat predictability in the system (Hoover 2003a, 2006) they spend less time defending territorial borders (i.e., “dear enemy”) (Fisher 1954; Temeles 1994; Frostman & Sherman 2004; Akçay et al. 2009). This extra time may allow males more opportunity to seek EP copulations, and males that know their neighbors may be generally ignored or undetected when intruding or near the periphery of their neighbors’ territories. In hooded warblers (*Wilsonia citrina*), Stutchbury (1998) found that when radio-tagged males made forays into neighboring territories containing fertile females, they typically went undetected by the resident male. There were no clear differences in male quality, but their prior experience on the site was not evaluated. If EP males are familiar with neighbors they may be able to better detect when male neighbors are away, which may provide enough opportunity to seek EP copulations. Several studies that detained territorial males found that neighboring

males were more likely to intrude and solicit the female for EP copulations once they detected his absence (Westneat 1992; Sundberg 1994; Dickinson 1997; Komdeur et al. 1999). Males with experience may also sing more if they spend less time in direct conflict with neighbors. In hooded warblers for example, males that sing more relative to their neighbors are more likely to be visited by neighboring females and gain EPFs with those females (Chiver et al. 2008). Regardless if males or females are more likely to foray and seek EPCs, it seems plausible that males that are familiar with their neighbors may be better at detecting and/or exploiting EP mating opportunities.

Conclusions

Westneat & Stewart (2003) in their review of the causes and correlates of EP paternity suggested that sexual conflict and the adaptations in all players (i.e., female, cuckolded male, & EP male) will likely lead to complex and highly variable rates and causes of EP mating. Understanding how each player's role causes conflict or contributes to the frequency of EP mating may provide new insights to the widespread patterns of multiple matings. In my study, the relative roles of breeding synchrony, breeding earlier than neighbors, and knowing your neighbors in explaining how site familiarity in males leads to more EPFs are yet to be determined. Nevertheless, whichever mechanism best explains the site familiarity advantage it seems plausible that increased EP mating opportunities as a result of reduced male breeding dispersal and site familiarity could be widespread among socially monogamous birds and potentially explain why the prevailing mating system tends to explain female-biased breeding dispersal in these species (Greenwood 1980; Greenwood & Harvey 1982). In addition, researchers who have identified male age as an important predictor of EP mating success and attributed it to "good genes" (Kleven et al. 2006; Bouwman et al.

2007; Schmoll et al. 2007) could in fact be missing the effect of prior breeding experience and site familiarity. Future research should try to address the roles of both site familiarity and age to determine whether prior breeding experience is important in other systems.

Table 6-1. Results of GLMM (binomial error and logit-link function) on the probability of gaining at least one EPF in year x by male prothonotary warblers ($n = 200$ males, $n = 294$ cases) in relation to level of experience on the site in year $x-1$, and number of actual neighbors and age category (1 year old, 2+ years old) in year x . Estimates for the repeated measures random effect* of individual (patch) by year are from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Level of experience in year $x-1$	$\chi^2_{2, 72} = 20.40$		< 0.0001
Not present on site		-1.928 ± 0.603	0.002
Bred on site, no EPFs		-0.297 ± 0.587	0.614
Bred on site, with EPFs		0	
Number of neighbors (0 to 6)	$\chi^2_{1, 72} = 14.46$	0.582 ± 0.153	0.0001
Removed variables			
Age	$\chi^2_{1, 71} = 0.72$		
1 year old		-0.515 ± 0.606	0.395
2+ years old		0	
Individual (patch) by year*	-----	0	-----

^a Estimates are on a log scale. Estimates of removed variables are from when they were added alone to the final model.

Table 6-2. Results of General linear mixed model on the number of neighbors in year x for male prothonotary warblers in relation to level of experience on the site in year $x-1$, and age category (1 year old, 2+ years old) and first clutch Julian day in year x . Final model includes a random effect for individual (patch) by year.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Level of experience in year $x-1$	$F_{2, 240} = 6.08$		0.003
Not present on site		-1.046 ± 0.324	0.001
Bred on site, no EPFs		-0.655 ± 0.331	0.045
Bred on site, with EPFs		0	
First clutch Julian day	$F_{1, 240} = 3.93$	-0.010 ± 0.005	0.049
Removed variables			
Age	$F_{1, 238} = 0.85$		
1 year old		0.205 ± 0.222	0.359
2+ years old		0	

^a Estimates of removed variables are from when they were added alone to the final model.

Table 6-3. Results of GLMM (Poisson error, log-link) on the number EP offspring lost to cuckoldry in year x for male prothonotary warblers in relation to level of experience on the site in year $x-1$, and age category (1 year old, 2+ years old), number of neighbors, condition and, infidelity of male (EPFs no, yes) in year x . Estimates for the repeated measures random effect of individual (patch) by year are from the final model.

Explanatory variables ^a	Test	Estimate \pm SE	p -value
Final model			
Number of offspring sampled	$X^2_1 = 22.16$	0.206 \pm 0.044	<0.001
Individual (patch) by year	$Z = 3.50$	1.657 \pm 0.475	<0.001
Removed variables			
EPFs (no, yes)	$X^2_1 = 1.24$	0.399 \pm 0.358	0.265
Level of experience in year $x-1$	$X^2_2 = 2.16$		0.339
Not present on site		0.739 \pm 0.521	
Bred on site, no EPFs		0.549 \pm 0.531	
Bred on site, with EPFs		0	
Number of neighbors (0 to 6)	$X^2_1 = 0.64$	0.089 \pm 0.111	0.424
Male condition	$X^2_1 = 0.13$	-0.050 \pm 0.137	0.715
Age 1 year old	$X^2_1 = 0.07$	0.073 \pm 0.270	0.788
2+ years old		0	

^a Estimates are on a log scale. Estimates of removed variables are from when they were added to the final model.

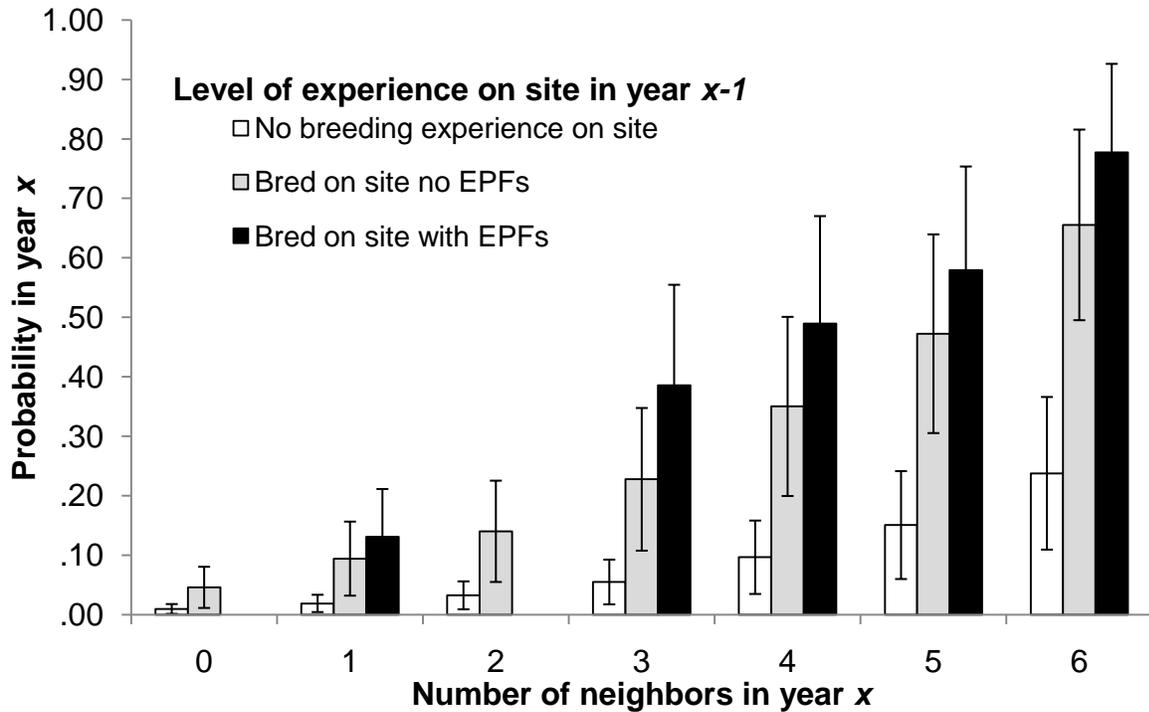


Figure 6-1. Estimates of the mean \pm 1 SE probability that a given male will gain at least one EP offspring in year x in relation to the number of neighbors and the level of breeding experience on the site in year $x-1$

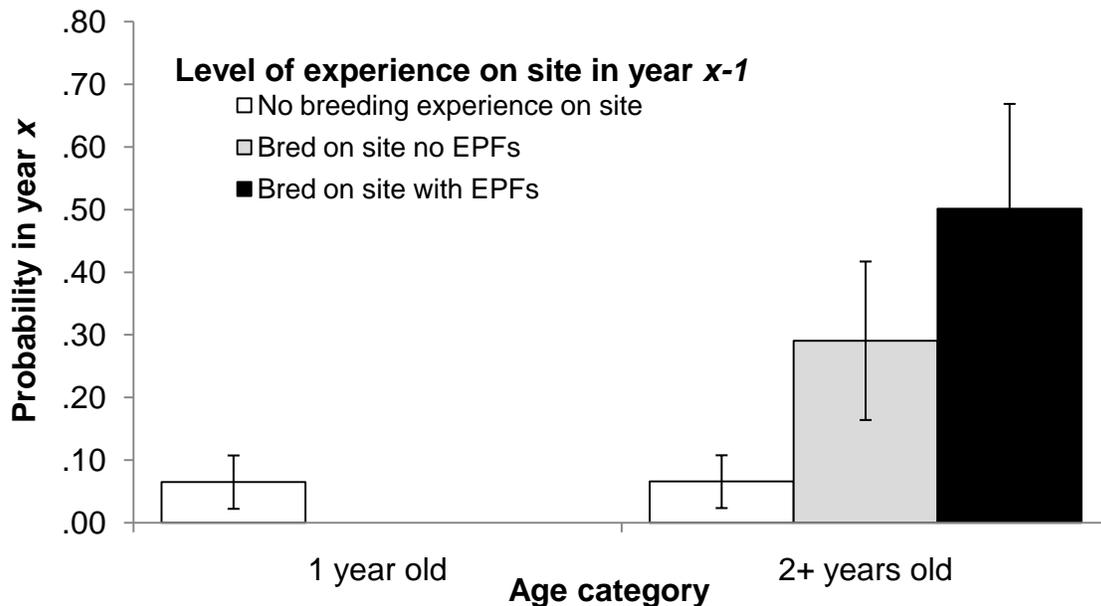


Figure 6-2. Estimates of the mean \pm 1 SE probability that a given male will gain at least one EP offspring in year x in relation to his age (1, 2+years) and the level of breeding experience on the site in year $x-1$

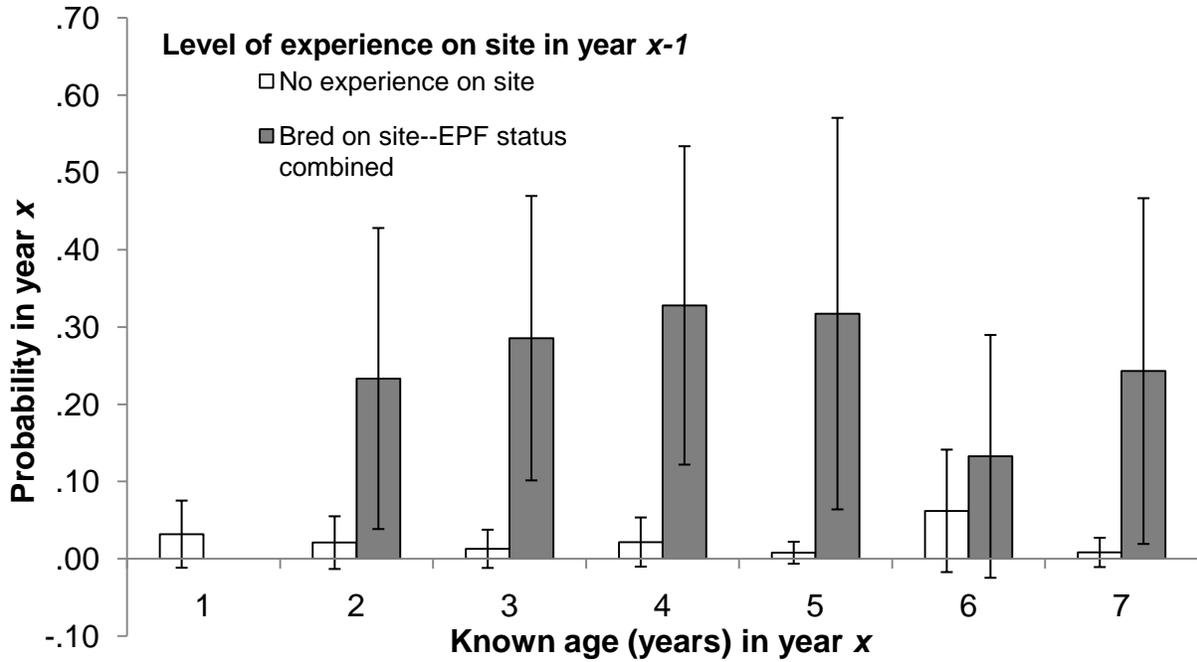


Figure 6-3. Estimates of the means \pm 1 SE probability that a given male will gain at least one EP offspring in year x in relation to his known-age (1 to 7 years) and the level of breeding experience on the site in year $x-1$

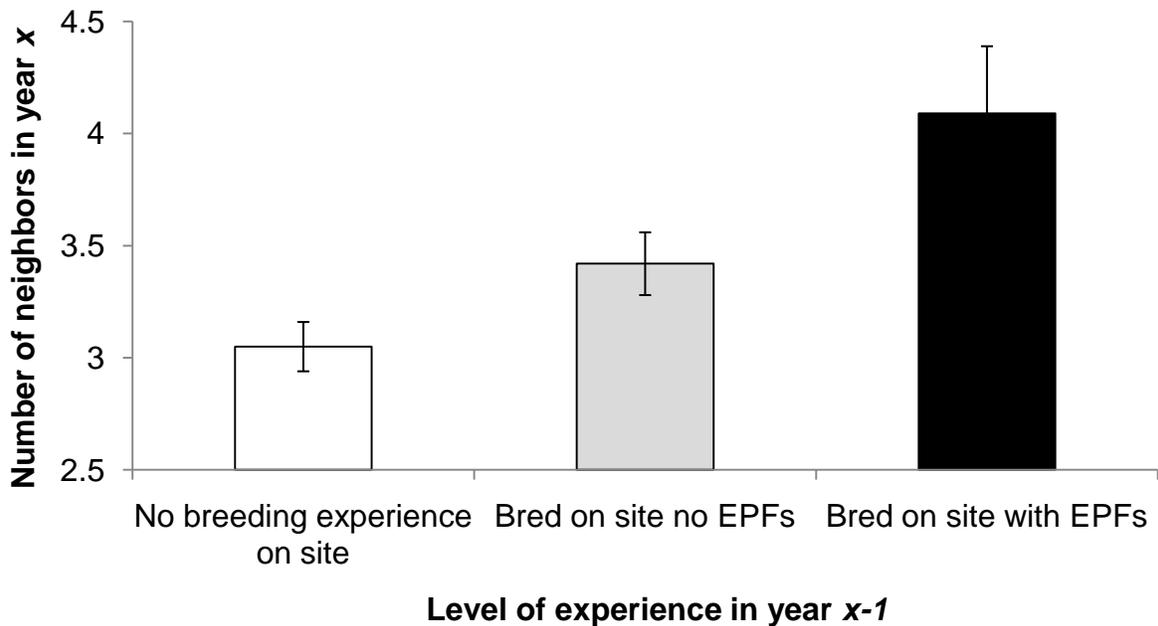


Figure 6-4. Estimated mean \pm 1 SE number of neighbors in year x for males with varying level of breeding experience on the site in year $x-1$.

CHAPTER 7 CONCLUSIONS

Mating System and Sex-Biased Breeding Dispersal

Advancing the Field

My dissertation research has advanced both our understanding of information use in breeding dispersal decisions of a socially monogamous, territorial songbird and a potentially widespread factor that explains sex-biased breeding dispersal in birds. For the past three decades, since Greenwood's (1980) seminal paper on mating systems and sex-biased dispersal few studies have identified clear quantifiable sex-specific fitness benefits of dispersal and philopatry. Greenwood suggested that the territorial sex, the less dispersive sex, must gain some benefit of returning to familiar places. As recently as 2009, however, researchers have referred to a presumed benefit of site familiarity to the territorial sex in studies on dispersal without having specific examples to which to refer. With my research, I have described a newly identified dispersal decision rule for males (the territorial sex in birds) that successfully fledged extra-pair (EP) offspring with neighbors. In addition, males that returned close to familiar places between years (typically after some EP mating success) gained an EP mating advantage, which ultimately yielded higher annual reproductive output. Females, in contrast, were more likely to disperse between years, and disperse farther based on their relatedness to their social mate, which was also related to cuckoldry. Hence, cuckoldry or EP mating has directly opposite effects on male and female dispersal decisions and conforms nicely to Greenwood's prediction that the prevailing mating system can explain patterns of sex-biased dispersal.

Public Information Collected at Sex-Specific Scales

In Chapter 2, I tested the hypothesis that male and female prothonotary warblers (*Protonotaria citrea*) use public information at two different scales by experimentally manipulating the reproductive success of focal pairs and conspecifics. I focused on unsuccessful pairs because they are some of the most likely individuals to use public information and determined whether conspecific reproductive success at the level of the neighborhood (i.e., adjacent neighboring territories) and/or the patch best explained breeding dispersal patterns for each sex. Unsuccessful males returned to the patch between-years based on the number of successful neighbors, whereas unsuccessful females returned to the patch based on public information available at a larger scale in the form of patch reproductive success (PRS). In addition, males were more likely to return to locations within their previous neighborhood than females. Dispersal distances decreased with neighborhood success in males and decreased with PRS in females, which corroborates my initial findings based on patch fidelity. In socially monogamous songbirds, males require territory or neighborhood-specific information because they select territories prior to the arrival of females. In contrast, if females return to good patches, they increase their likelihood of choosing a good territory simply because males are already defending the best-quality territories. Thus males and females seem to rely on or collect public information at different scales (e.g., patch vs. neighborhood). Most studies, to date, have neglected to examine sex differences in the use of public information because the origin of the dispersers is typically unknown. Sex differences in the scale at which public information is gathered can help explain widespread patterns of sex-biased breeding dispersal in territorial, socially monogamous songbirds.

Neighborhood Fidelity of Unsuccessful Males: A Role for Neighbors and Extra-Pair Mating

Dispersing individuals, often those that have bred unsuccessfully may rely on public information (i.e., conspecific reproductive success) to assess habitat quality. An alternative hypothesis is that males unsuccessful in their own nests may rely on private information in the form of extra-pair (EP) mating success. In Chapter 3, I experimentally tested the hypothesis that unsuccessful male prothonotary warblers (*Protonotaria citrea*) would be more likely to fledge EP offspring with an increase in the number of successful neighbors, and this in turn would increase male neighborhood fidelity relative to those males without EP mating success. The probability a male fledged EP offspring increased with the number of successful neighbors. “Unsuccessful” males were twice as likely to return to their neighborhood if they fledged at least one EP offspring compared to those males that did not fledge EP offspring. Unsuccessful males without EP offspring relied on public information and returned to their neighborhood based on the number of successful neighbors. Females in my system cannot increase their reproductive output outside of their own breeding attempts, whereas males may significantly increase their lifetime reproductive success by returning to locations where they have fledged EP offspring. This is the first study to experimentally demonstrate that EP mating success influences male breeding dispersal decisions. Extra-pair mating success significantly reduced dispersal of unsuccessful males and therefore could be a major factor influencing sex-biased breeding dispersal in this and other socially monogamous species.

Female Relatedness to Social Mate Increases Cuckoldry and Between-Year Breeding Dispersal

Natal dispersal, in many systems, may be insufficient to eliminate all incestuous matings. Mating with close relatives is costly because it may lead to inbreeding depression. In socially monogamous species, female promiscuity may alleviate mating with relatives whereas between-year breeding dispersal may provide an additional means of avoiding closely related mates. In Chapter 4, I experimentally tested the hypotheses that female prothonotary warblers (*Protonotaria citrea*) would be more likely to cuckold a closely-related mate, and that their between-year breeding dispersal would increase the more related they had been to their social mate. Females were experimentally manipulated to fail in their breeding attempts so that territory quality did not limit their propensity to disperse. The probability of females cuckolding their social mate increased with relatedness. In addition, the proportion of offspring in a female's nest sired by an extra-pair male increased with female relatedness to her social mate. Cuckoldry provided a within-season means of reducing offspring homozygosity which tended to increase offspring condition. Between-year patch fidelity for females that cuckolded their mate was nearly twice as high compared to those females that did not cuckold their mate. Between-year breeding dispersal distances, however, were best predicted by a female's relatedness to her previous social mate regardless of whether she cuckolded him or not. Between-season divorce was associated with longer dispersal distances and was effective at reducing the likelihood of females re-pairing with a closely related mate. Whether females have the immediate ability to determine how closely related they are to a particular male is uncertain and unlikely, but must be considered in the future. In prothonotary warblers, and other socially monogamous

species, female promiscuity and between-year breeding dispersal are effective adaptations to alleviate pairings with close relatives and decrease the risks of inbreeding.

Experimental Evidence that Males Monitor the Outcome of their Extra-Pair Offspring

Realized reproductive success can vary dramatically for individual males of many species. Extra-pair (EP) mating opportunities can create significant variance in male reproductive output. Therefore, there should be strong selection for traits or behaviors that increase a male's ability to identify good mating opportunities. What is not known is to what degree males are aware of their EP mating success and how this influences future breeding decisions. In Chapter 5, I tested the hypothesis that male prothonotary warblers (*Protonotaria citrea*) could accurately assess their own reproductive success via EP mating. I exploited a breeding dispersal decision rule identified from my system where males returned to neighborhoods where they had successfully fledged EP offspring. What was not known was whether males responded to simply copulating with an EP female, or if males were actually aware of their EP offspring fledging. I experimentally manipulated neighborhoods of focal males such that each male had a variable number of successful neighbors. Consequently, only males with EP copulations/fertilizations (EPCs/EPFs) with successful neighboring females would perceive their EP offspring as fledged. Those with EPCs/EPFs with unsuccessful neighbors would not increase their realized reproductive success. Males that successfully had EP offspring fledge (EPYs) produced two more offspring on average than those without EPFs or those with EPFs but no EPYs. Males gaining EPYs subsequently returned to their neighborhoods at nearly twice the rate (~90%) compared

to those without EPFs (47%) and those males with EPFs but not EPYs (47%). This result demonstrates that males are not only aware of their EP copulations with particular females, but they follow the fate of those offspring to failure or fledging. If EPCs are a good predictor of EPFs then simply copulating with a particular female would provide adequate information about their EP paternity. If EPCs are widespread, however, other mechanisms such as kin recognition may be involved.

Male Benefits of Site Familiarity

Sex-biased breeding dispersal is widespread and is likely associated with the prevailing mating system. In birds, females are more dispersive because presumably males, the territorial sex, benefits from site familiarity. Despite this long-standing theory, few studies have identified male-only fitness benefits of returning to a familiar place. Age and experience are often correlated and age is commonly associated with extra-pair (EP) mating success. In Chapter 6, I experimentally examined the hypothesis that male prothonotary warblers (*Protonotaria citrea*) that return to familiar sites rather than simply being older gain a fitness advantage in the form of EP fertilizations. Males were randomly selected to produce offspring in their own nest, be surrounded by variable numbers of successful neighbors, and indirectly selected to have EP offspring fledge from a neighbors nest. These experimental manipulations subsequently influenced male neighborhood fidelity in the next. By influencing return rates of males, I eliminated or reduced the confounding factor of male quality on EP mating success. Males in that returned to a familiar site between years and males in larger neighborhoods were significantly more likely to gain EPFs than males that were new to a site, regardless of age. A known-age (1 to 7 years old) analysis confirmed this finding and showed that male age, in no way, influenced their probability of EP mating success after accounting

for breeding experience on the site. Older males (2+ years old), however, started breeding earlier than younger males (1 year old), but experience and not age best predicted the size of a males neighborhood. Neither level of experience on a site nor age influenced the probability of being cuckolded by their social mate, which demonstrates that males familiar with a site sired more offspring on average. This is the first study to disentangle the effects of site familiarity and age on EP mating success. Increased EP mating opportunities as a result of reduced male breeding dispersal and site familiarity could be widespread among socially monogamous birds and potentially explain why the prevailing mating system tends to explain female-biased breeding dispersal in socially monogamous birds

APPENDIX: SUPPLEMENTARY MATERIALS

The following materials include figures with the original observed data that was used to construct the various multivariate models reported in each chapter. In all figures, values are summarized from or are the original counts or values based on individual samples and are not controlled by site, year or other random effects unless otherwise stated.

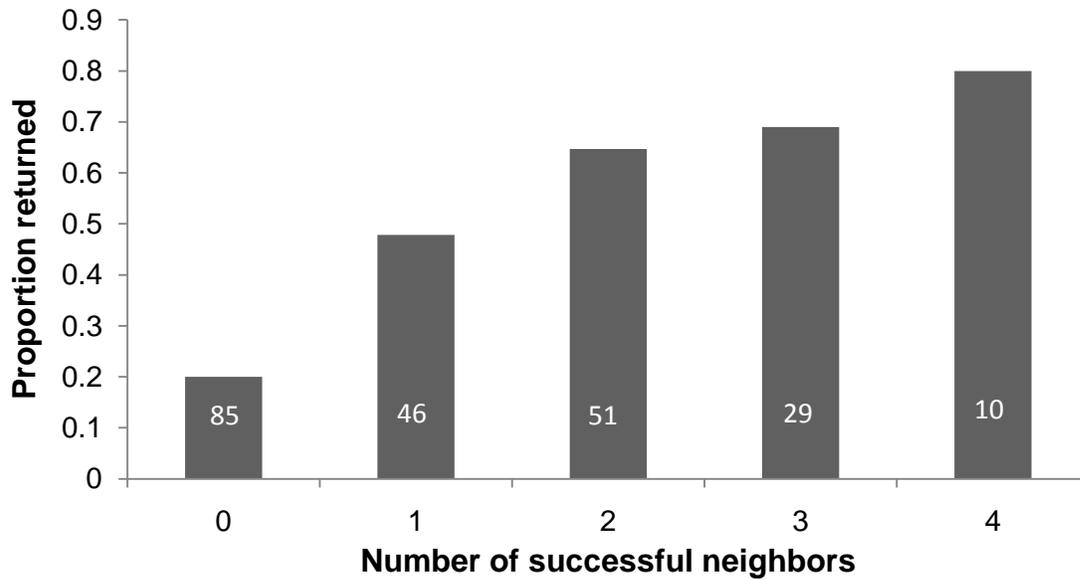


Figure A-2. The actual proportion of unsuccessful male prothonotary warblers that returned to their site between years based on the number of successful conspecific neighbor pairs. Numbers within bars represent the total number of males sampled in each group.

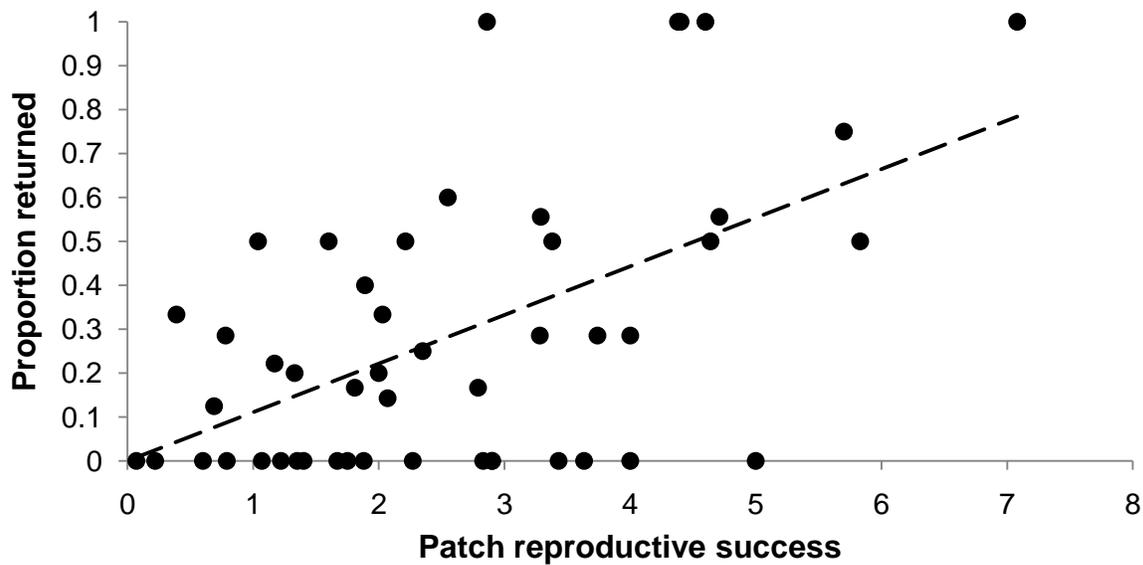


Figure A-3. The actual proportion of unsuccessful female prothonotary warblers that returned to their site between years based on conspecific reproductive success on the patch. Each point represents the proportion of females that returned to a particular site in a given year.

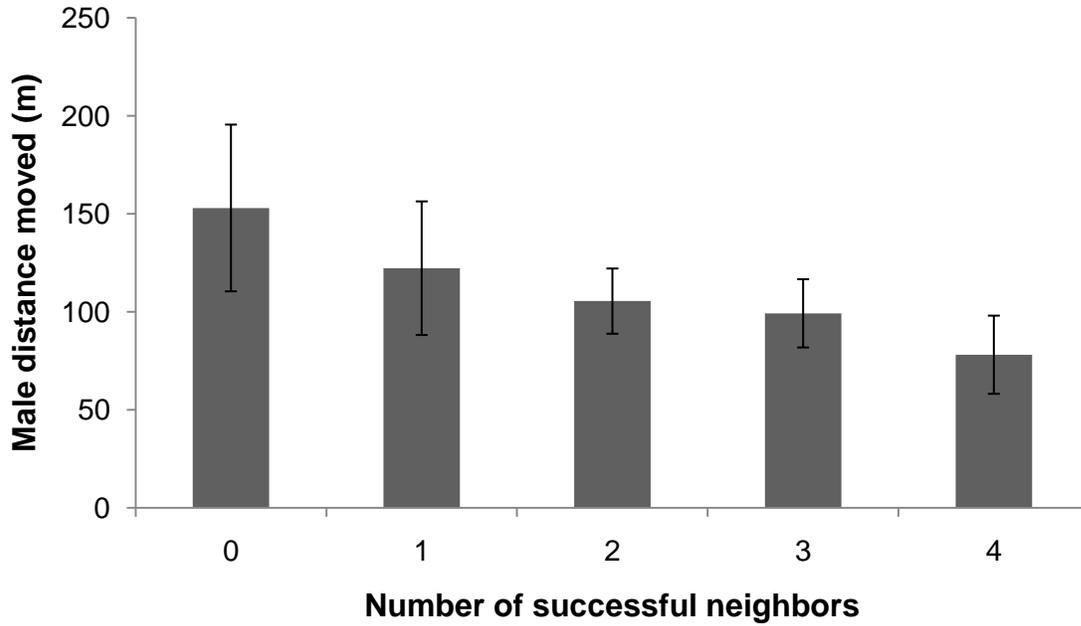


Figure A-4. The actual distance moved (mean \pm SE) between years of unsuccessful male prothonotary warblers based on the number of successful conspecific neighbor pairs.



Figure A-5. The actual distance moved between years of unsuccessful female prothonotary warblers based on the reproductive success of conspecifics on the patch.

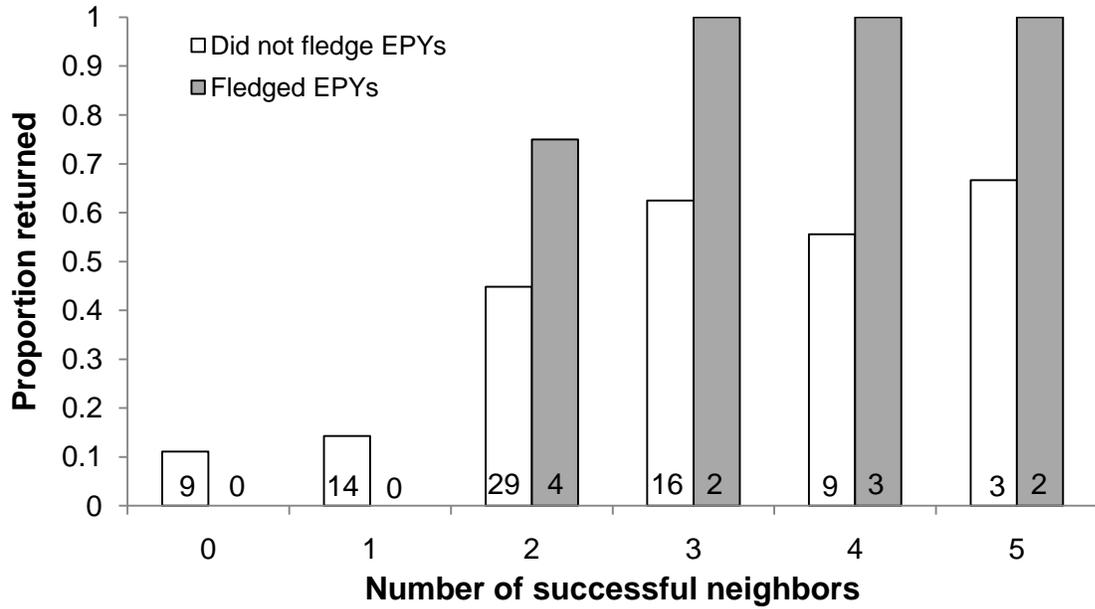


Figure A-6. The actual proportion of unsuccessful male prothonotary warblers that returned to their neighborhoods between years based on the number of successful neighbors and whether they had extra-pair young (EPYs) fledge from a neighbors nest. Numbers inside bars represent the total number of males in each category.

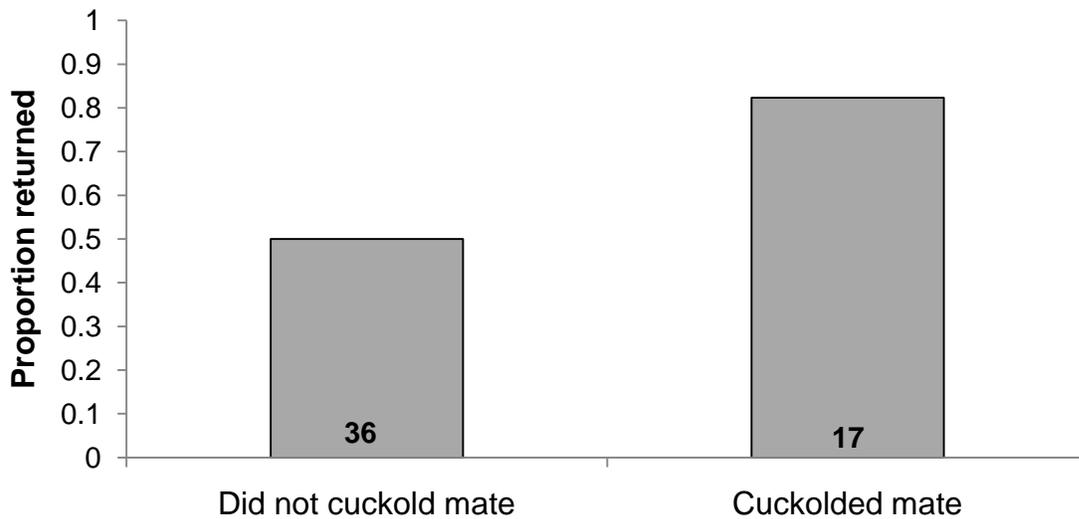


Figure A-7. The actual proportion of unsuccessful female prothonotary warblers that returned to their patch between years based on whether they cuckolded their social mate or not. Numbers inside bars represent the total number of females in each category.

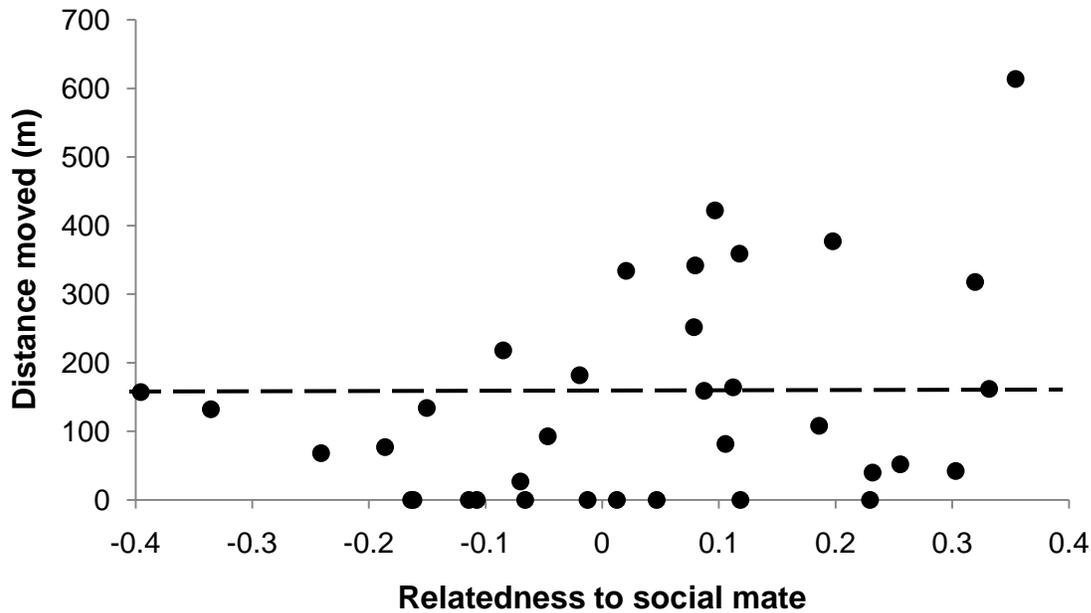


Figure A-8. Actual distances moved (m) between years by unsuccessful female prothonotary warblers based on their relatedness to their social mate in the previous year. Dotted line represents the approximate distance to the boundary of the neighborhood

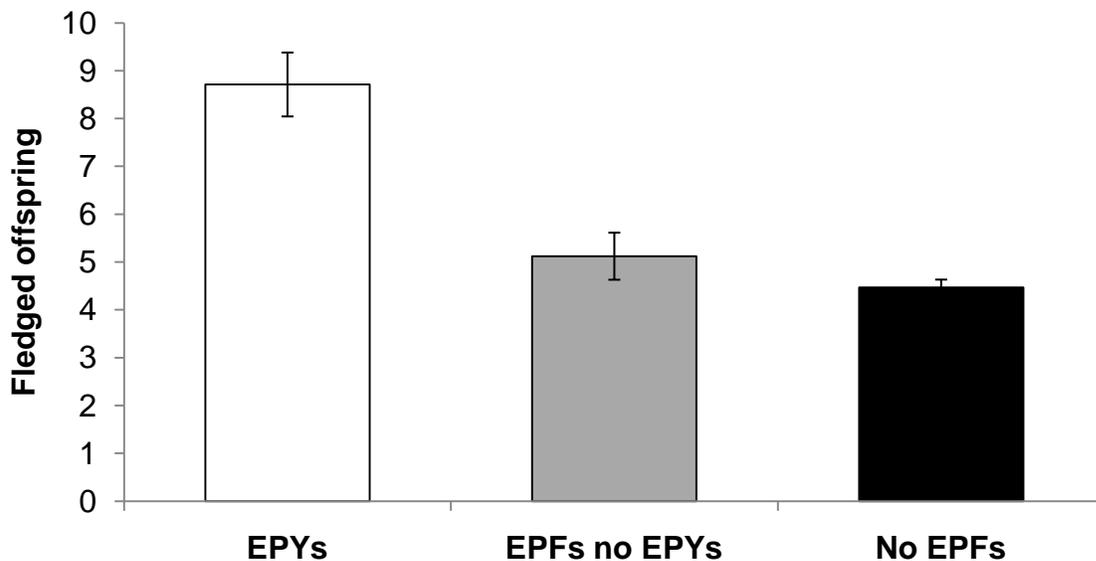


Figure A-9. Actual number (mean \pm SE) of fledged prothonotary warbler offspring (realized reproductive success) by males based on male extra-pair mating success. Values take into account only those offspring both sired and fledged from a male's own nest plus those EPYs fledged from neighboring nests. EPYs = extra-pair offspring fledged, EPFs no EPYs = extra-pair fertilizations with unsuccessful neighbor, and No EPFs = no extra-pair fertilizations.

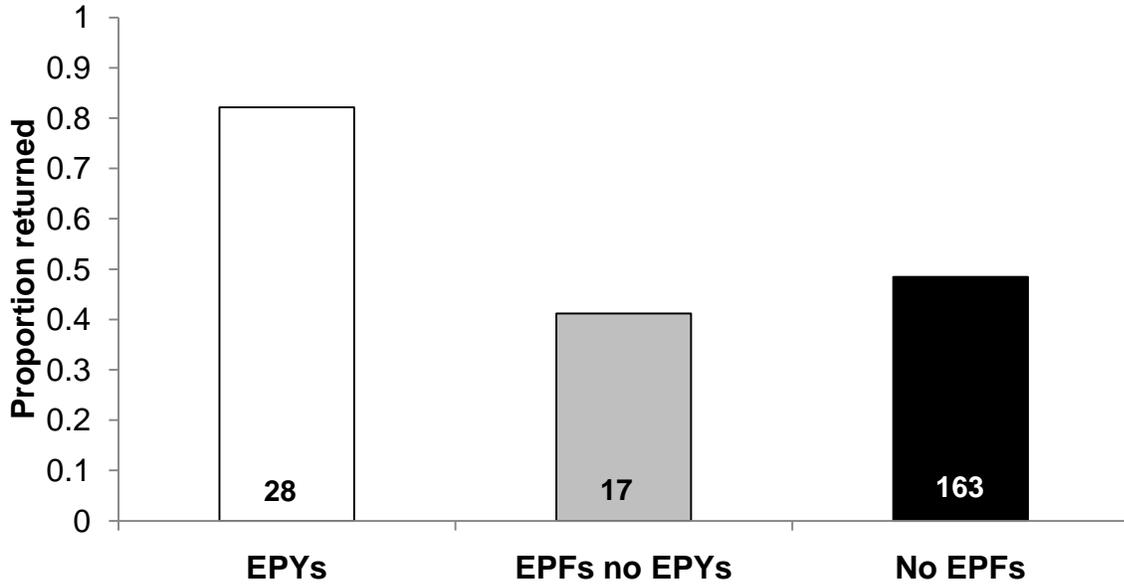


Figure A-10. Actual proportion of prothonotary warbler males that returned to their neighborhoods between years based on their extra-pair mating success. EPYs = extra-pair offspring fledged, EPFs no EPYs = extra-pair fertilizations with unsuccessful neighbor, and No EPFs = no extra-pair fertilizations. Numbers in bars represent the total number of males in each category

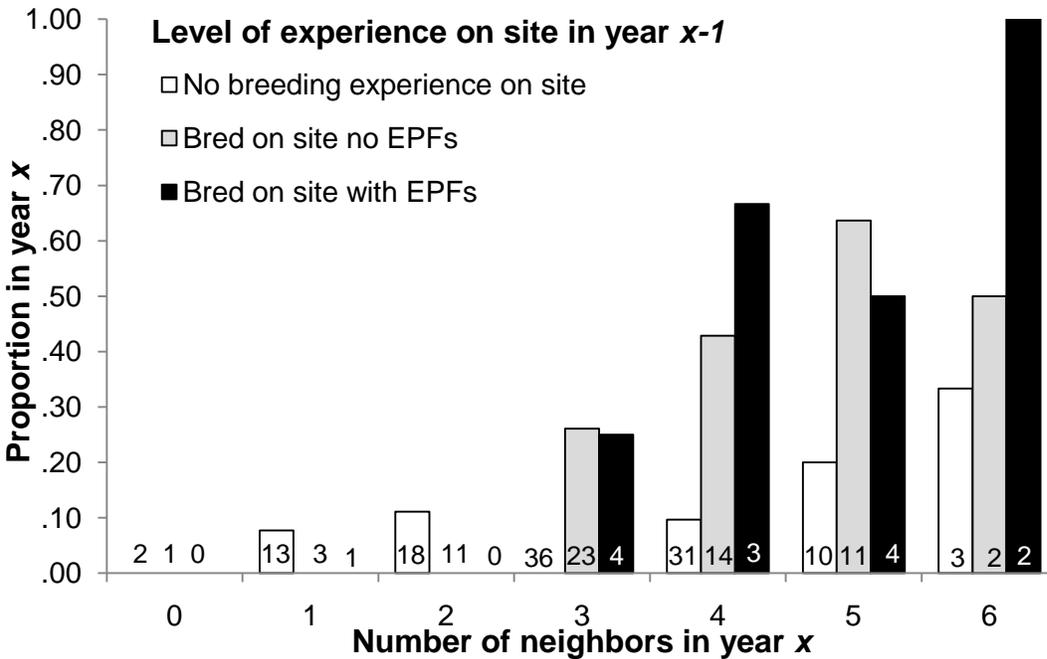


Figure A-11. Actual proportion of prothonotary warbler males that successfully gained at least one EPF in year $x + 1$ based on the size of their neighborhood and level of experience in year x . Numbers in bars represent the total number of males in each category

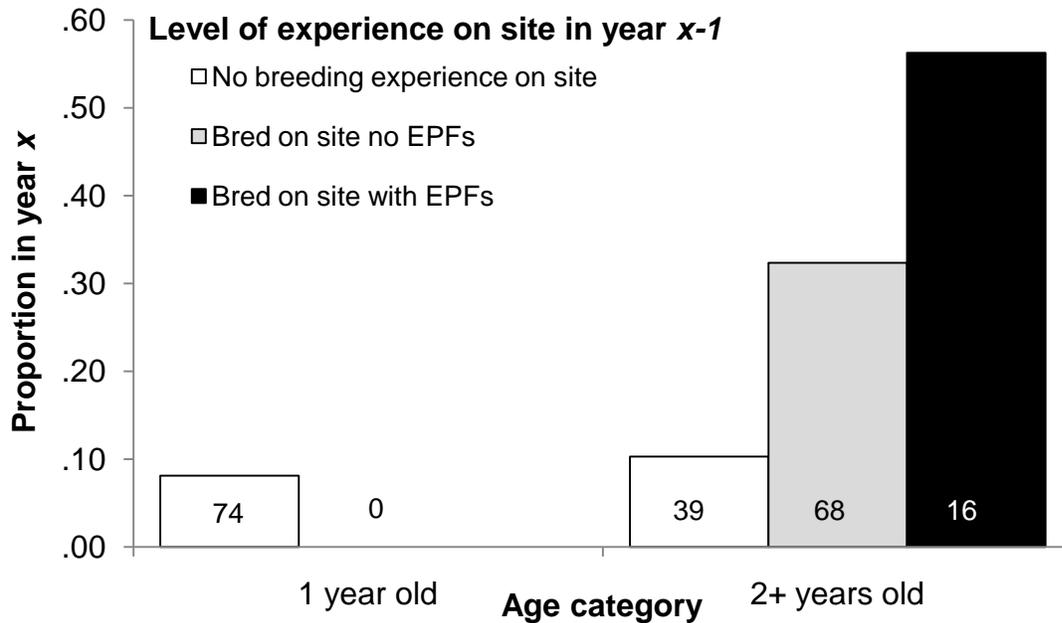


Figure A-12. Actual proportion of prothonotary warbler males that successfully gained at least one EPF in year x based on their age category and level of experience in year x . Numbers in bars represent the total number of males in each category

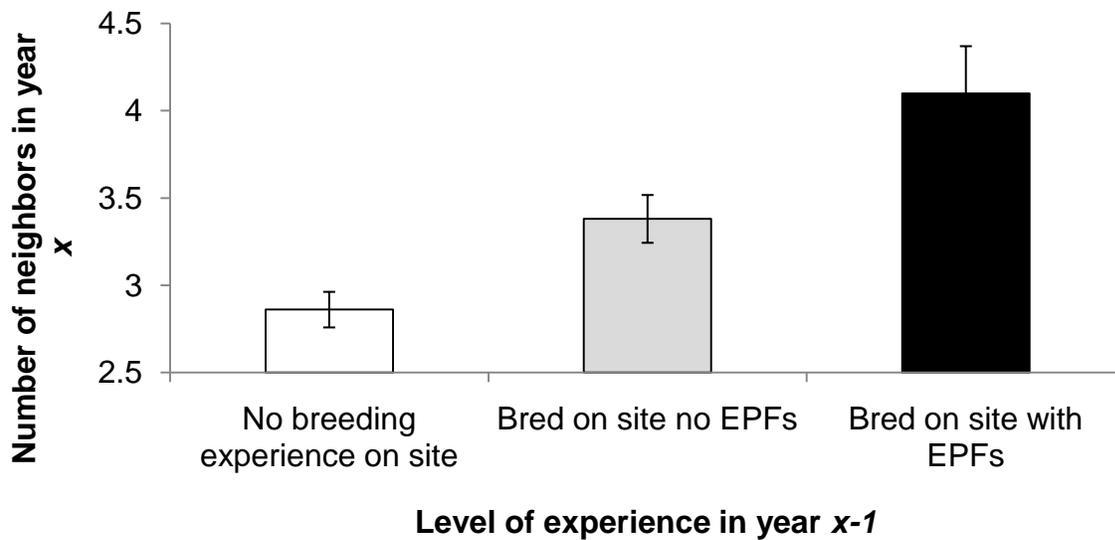


Figure A-13. Actual number of neighbors in year x for male prothonotary warbler based on level of experience in year $x-1$. Numbers in bars represent the total number of males in each category

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BIOGRAPHICAL SKETCH

Wendy M. Schelsky was born in Park Ridge, Illinois, USA in 1971. In 1993, she graduated with a Bachelor of Science degree specializing in biological sciences (concentration: zoology) from Colorado State University in Fort Collins, Colorado. Upon graduation, she took the next four years to gain experience in biological research throughout the United States and abroad. In 1999, she entered graduate school at the University of Illinois-Urbana-Champaign in the Department of Animal Biology. In August 2003, she graduated from the University of Illinois with her Master of Science degree and entered the graduate program in the Department of Zoology at the University of Florida, Gainesville, Florida to pursue her Doctor of Philosophy. Post-degree she will work as a Post-Doctoral researcher at the Institute of Natural Resource Sustainability at the University of Illinois-Urbana-Champaign and will work on several conservation genetics projects throughout the state of Illinois.