INFLUENCES OF PERSONAL INFORMATION, PUBLIC INFORMATION, AND EXTRA-PAIR PATERNITY ON BREEDING SITE FIDELITY IN A SONGBIRD

A Dissertation

by

ANDREW JAMES CAMPOMIZZI

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

DOCTOR OF PHILOSOPHY

August 2011

Major Subject: Wildlife and Fisheries Sciences

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Approved by:

Chair of Committee,	Michael L. Morrison
Committee Members,	James C. Cathey
	Kevin J. Gutzwiller
	Gil Rosenthal
Head of Department,	Thomas E. Lacher Jr.

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ABSTRACT

Influences of Personal Information, Public Information, and Extra-pair Paternity on
Breeding Site Fidelity in a Songbird. (August 2011)
Andrew James Campomizzi, B.S., University of Dayton; M.S., Texas A&M University
Chair of Advisory Committee: Dr. Michael L. Morrison

I investigated the role of extra-pair paternity on use of public information and the interaction between public information and personal information for patch fidelity decisions. It is unknown if songbirds use public information about the number of conspecific fledglings for patch fidelity decisions when extra-pair paternity is uncommon. I tested if probability of patch fidelity was associated with (1) number of fledglings in adjacent territories (public information), and (2) number of fledglings raised with a social mate (personal information). I used logistic regression to predict probability of patch fidelity of males and females based on the 2 uncorrelated predictor variables (Spearman's rank correlation, $S = 21895.28$, $n = 50$, $P = 0.723$, $r = –0.051$).

I monitored patch fidelity of 107 territories, counted the number of fledglings in each territory, and assessed parentage of 102 young from 36 nests for white-eyed vireos (*Vireo griseus*) from 2008–2010 in a 100 ha patch of woodland in central Texas, USA. I excluded the social male as the father of 3 of the 102 young and did not exclude any of the social females as the mother with parentage analysis using 6 microsatellite loci. The number of fledglings in adjacent territories was not a good predictor of probability of patch fidelity for males ($\beta_1 = 0.166$, df = 35, $P = 0.247$, Nagelkerke's $R^2 = 0.054$) or females ($\beta_1 = 0.121$, df = 17, $P = 0.670$, Nagelkerke's $R^2 = 0.016$). The number of fledglings raised with a social mate was also not a good predictor of probability of patch fidelity for males ($\beta_1 = -0.296$, df = 43, $P = 0.360$, Nagelkerke's $R^2 = 0.029$), whereas it was a good predictor for females ($\beta_1 = 1.281$, df = 21, $P = 0.048$, Nagelkerke's $R^2 = 0.409$).

The dominant ecological concepts for explaining site fidelity in songbirds, win-stay lose-switch (based on personal reproductive success with a social mate) and public information, were not good predictors probability of patch fidelity well for male white-eyed vireos. The win-stay lose-switch model, but not public information, was a good predictor of probability of patch fidelity for females. My results suggest that use of public information may depend on frequency of extra-pair paternity. Males may primarily use other information for patch fidelity decisions beyond reproductive success of conspecifics for patch fidelity decisions in some circumstances. My results support the need to ensure high levels of nesting success for females to return and maintain populations in areas managed for breeding songbirds for conservation efforts to be successful.

ACKNOWLEDGEMENTS

I thank the Department of Defense, Integrated Training and Management (ITAM), Office of the Secretary of Defense; Texas Parks and Wildlife Department; and the Tom Slick Senior Graduate Fellowship, College of Agriculture, Texas A&M University for financial support of my research. The Institute of Renewable Natural Resources, Texas A&M University, provided additional support.

I thank my committee members (M. L. Morrison, J. C. Cathey, G. Rosenthal, and K. J. Gutzwiller) for their invaluable guidance when I may have strayed, my collaborator, J. A. DeWoody and members of his lab at Purdue University, for their boundless knowledge of working with DNA, genotyping, and parentage analysis, and R. N. Wilkins and the Institute of Renewable Natural Resources at Texas A&M University for making it all possible. I also thank landowners and managers for graciously allowing access to their properties for field work on small, but noisy birds, J. Assmus, A. Nakamura, W. Rodriguez, J. Hill, J. Rentsch, E. Cord, and Z. Primeau for countless hours of assistance collecting field data in oppressive heat, B. Hays, S. Manning, L. Law, V. McCallister, V. Buckbee, and M. Rubio for logistic support and translations between a Yankee scientist and Texas ranchers, B. A. Collier for guidance on analyses and my forays into using R, M. Mateos and L. Hurtado for allowing me to use their software for genotyping analyses; J. Detwiler for double checking my scoring of alleles, and many graduate students in the Morrison lab for assistance solving problems big and small. Careful readings and thoughtful comments by S. L. Farrell, M. E. Marshall, J. A. DeWoody, and B. A. Collier improved this manuscript.

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1. INTRODUCTION

Habitat selection is a process used by individuals, influenced by behavioral and environmental factors, resulting in distribution patterns observed by researchers (Jones 2001). Natural selection should cause individuals to select breeding habitat that maximizes reproductive success (Fretwell and Lucas Jr. 1969; Hilden 1965; Martin 1993) within given genetic constraints of a species (Gould and Lewontin 1979) and inability to maximize all reproductive parameters. Most habitat selection research has focused on examining associations between animal locations and vegetation characteristics (Arlt and Part 2007; Misenhelter and Rotenberry 2000) or manipulating various aspects of a species' habitat (Fontaine and Martin 2006; Petit and Petit 1996) to identify mechanisms involved in habitat selection and fitness outcomes resulting from those decisions. The role of behavioral mechanisms in habitat selection, such as con- and heterospecific attraction, appears to be gaining support in the literature compared with the more traditional focus on vegetation only (Ahlering and Faaborg 2006; Betts et al. 2008; Nocera and Betts 2010).

Territorial songbirds can use personal and public information (Doligez et al. 2002; Valone and Templeton 2002) to make habitat selection decisions. Public information is likely to be the most useful behavioral component used for habitat selection (Danchin et al. 2001) because it enables individuals to assess habitat quality, in terms of fitness consequences, by observing experiences of other individuals (Bonnie and Earley 2007). Personal information is limited to what an individual can experience

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This dissertation follows the style of Behavioral Ecology.

on its own (e.g., visiting various trees to determine where to forage; Dall et al. 2005), whereas public information is much broader, including all information an individual can gather by observing others that relates to habitat quality in terms of subsequent fitness (e.g., observing where other individuals are foraging to determine where to find food; Boulinier and Danchin 1997; Danchin et al. 2004).

The number of fledglings raised with a social mate and the number of fledglings observed in neighboring territories of conspecifics is perhaps the information most readily available to songbirds for assessing habitat quality during the breeding season. The number of fledglings is a measure of habitat quality and is the result of physical and biological conditions of a breeding site (Boulinier and Danchin 1997; Klopfer and Ganzhorn 1985). The number of heterospecific fledglings in adjacent territories may also play a role in an individual's assessment of habitat quality (Parejo et al. 2004; Seppanen et al. 2007), but currently there is little information in the literature, mostly restricted to habitat copying (Forsman and Thomson 2008) and heterospecific attraction (Fletcher 2007). Understanding the relative influences of personal and public information for selection of breeding habitat is important for understanding why and under what conditions individual songbirds make particular selection decisions.

Previous research about the presence and number of fledglings in adjacent territories has not addressed the possibility that extra-pair paternity may play a role in the use of that information. Previous research has operated under the assumption that if an individual male observes the number of fledglings in neighboring territories that the individual is only assessing habitat quality as indicated by the presence, number, and body condition of fledglings. Extra-pair paternity is common among neighboring territories (Bollinger and Gavin 1991; Neudorf et al. 1997; Stutchbury 1998; Webster et al. 2001) in many songbird species (Griffith et al. 2002), suggesting that by assessing the number of fledglings in adjacent territories, individual males may actually be assessing their own fitness in circumstances with frequent extra-pair paternity. Thus, what researchers previously thought was public information may, in some cases, be personal information.

Adult female use of the number of fledglings in adjacent territories provides a contrast with that of males because females cannot have breeding success in an adjacent territory through extra-pair paternity, but may use the number of fledglings in adjacent territories as an indicator of habitat quality. Although females cannot produce fledglings in adjacent territories through extra-pair copulations, females can achieve the same end through conspecific brood parasitism (laying an egg in the nest of a conspecific). This behavior occurs in some songbirds (Yom-Tov 2001), however the frequency of occurrence is not well known. Thus, if females use the presence of fledglings in adjacent territories for habitat selection in the subsequent year, it is more likely they use the presence of fledglings as an indicator of habitat quality, not personal reproductive success.

A fact often ignored in studies of habitat selection is that many individuals simply return to breed in the same location as the previous year (i.e., breeding site fidelity). Most research on site fidelity has focused on understanding the role of personal reproductive success with a social mate (Bollinger and Gavin 1989; Greenwood and Harvey 1982; Haas 1998; Hoover 2003). Some computer-based modeling suggests adults exhibit site fidelity when individuals are able to fledge young with a social mate and disperse to other breeding sites when unable to fledge young (i.e., the win-stay, lose-switch strategy) if habitat quality is temporally auto-correlated among years (Schmidt 2001; Switzer 1993). Some empirical studies of breeding site fidelity support the win-stay, lose-switch strategy to some extent for females only (Sedgwick 2004) or for both males and females (Gavin and Bollinger 1988; Greenwood and Harvey 1982; Haas 1998; Hoover 2003; Sedgwick 2004). However, about 20–50% of songbirds exhibit site fidelity even when not successfully fledging young with a social mate (Bollinger and Gavin 1989; Haas 1998; Hoover 2003).

Other computer-based modeling has suggested an alternative strategy of deciding site fidelity based on breeding success of conspecifics in a patch rather than personal reproductive success with a social mate if the environment is patchy and habitat quality is temporally auto-correlated (Boulinier and Danchin 1997). Thus, an individual may exhibit site fidelity even if it did not successfully reproduce with a social mate because public information indicates good habitat quality based on the number of fledglings in neighboring territories.

Site fidelity has been associated with breeding success of conspecifics in neighboring territories in some studies. For example, Hoover (2003) found that for unsuccessful territories, 51% of male prothonotary warblers (*Protonotaria citrea*) returned to the same patch during the subsequent year if their neighbors successfully raised young, versus 16% returns for those with unsuccessful neighbors. Similarly, songbirds can use the presence (Bollinger and Gavin 1989) and body condition of young in adjacent territories as a reliable indicator of habitat quality (Danchin et al. 2004; Doligez et al. 2003; Doligez et al. 2002). However, as noted above, an individual's, especially a male's, assessment of the number of fledglings in neighboring territories may indicate habitat quality and or personal reproductive success through extra-pair paternity (suggested by Hoover 2003).

To my knowledge, no study has examined if males use public information, specifically the number of fledglings in adjacent territories, differentially depending on paternity for site fidelity decisions. I found only 2 species, collared flycatcher (*Ficedula albicollis*) and black-throated blue-warbler (*Dendroica caerulescens*), were used for studies examining site fidelity and reproductive success of neighboring conspecifics. Both species had common extra-pair paternity in other studies with, 33 and 34%, respectively, of broods with ≥1 young of extra-pair paternity (Griffith et al. 2002). Thus, it is currently unknown if individuals will use reproductive success of neighbors for site fidelity decisions in species or conditions with uncommon extra-pair paternity.

Studies of site fidelity typically present results as a percent of individuals returned given particular circumstances (e.g., 50% of males that fledged ≥1 young returned). A potentially more informative approach, and the one I took here, was to predict a probability of patch fidelity, given various circumstances experienced by the birds. This approach enables a more nuanced investigation of patterns of patch fidelity, quantifying the chance of a male or female returning given some set of circumstances. To my knowledge no study has investigated how probability of patch fidelity of an individual changes given the number of fledglings in adjacent territories, or the number of personal fledglings with a social mate, or a combination of the public and personal information about the number of fledglings.

I investigated the role of extra-pair paternity on use of public information and the interaction between public information and personal information, based on the number of fledglings in territories, for patch fidelity of white-eyed vireos (*Vireo griseus*). It is likely that extra-pair paternity is uncommon in white-eyed vireos because breeding is asynchronous (Morton et al. 1998), due to common nest failure and subsequent re-nesting (Campomizzi et al. 2009; Conkling 2010), and the high level of paternal care (Hopp et al. 1995; Møller 2000). Although various species of songbirds would potentially be useful in this study, I selected this species because much is known about their breeding biology (Hopp et al. 1995), nests are typically within 2 m of the ground making monitoring practical, adults can be captured and marked, and microsatellite markers are available for genotyping (Barr et al. 2007). My objectives were to:

1. Determine whether probability of patch fidelity of males was associated with the number of fledglings in adjacent territories (i.e., territories sharing a boundary) when extra-pair paternity was rare. If an association occurred, then it supports the use of public information as an assessment of habitat quality. Alternatively, the lack of an association may suggest males assess the number of fledglings in adjacent territories depending on paternity.
2. Determine whether probability of patch fidelity of males and females was associated with the number of fledglings in adjacent territories. If there was

an association for both sexes it supports the general use of public information as an assessment of habitat quality.

3. Evaluate the importance of the number of fledglings in adjacent territories depending on whether an individual fledged young with a social mate for explaining patch fidelity for adult males and females.

2. METHODS

Study Area

I studied white-eyed vireos nesting in a 100 ha patch of mature, oak-juniper (*Quercus-Juniperus*) woodland in the Leon River watershed in central Texas, USA. I used a focal area of about 60 ha where I attempted to monitor all white-eyed vireos and then searched throughout the 100 ha patch for individuals that exhibited patch fidelity. I selected this study area because long term access was granted and I expected to find enough territories (about 50) to study site fidelity patterns given available effort and logistical constraints. Common land uses in the watershed were ranching, farming, and hunting. The most common trees species in this patch of woodland were juniper species (*Juniperus spp.*), Texas oak (*Quercus buckleyi*), Carolina buckthorn (*Frangula caroliniana*), and cedar elm (*Ulmus crassifolia*). Oak-juniper woodlands in this watershed are found in canyons among mesas with elevation 200–500 m. The 30-year-normal annual rainfall was 84.68 cm and rainfall was 85.19 cm in 2008, 95.33 cm in 2009, and 101.85 cm in 2010 (NOAA 2011). Average temperature for 30-year-normal was 25.5°C and average annual temperature was 19.4°C in 2008, 19.9°C in 2009, and 19.6°C in 2010 (NOAA 2011).

Study Species

White-eyed vireos are neotropical migrants that breed in the eastern half of the U.S. from March–August and winter or are present year-round along the Atlantic coast of the southeastern U.S.; the coast of the Gulf of Mexico in the U.S., Mexico, and northern Central America; and in parts of the Bahamas and Greater Antilles (Hopp et al. 1995). I assumed site fidelity patterns in the patch of woodland used for my study were not unique because individuals were not genetically or socially isolated in this location. White-eyed vireos are one of the most common songbirds in the woodlands and shrublands in the 414,265 ha Leon River watershed and can immigrate to and emigrate from patches of woodland within and among years. As is common in many songbird species, nest predation is the primary cause of nest failure in white-eyed vireos in my study area (Campomizzi et al. 2009; Conkling 2010) and has shown weak associations with vegetation within a patch (Conkling 2010).

Male Patch Fidelity

Patch fidelity

During March–July, I recorded the number of fledglings in territories in 2008 and 2009, and patch fidelity from 2008–2009 and 2009–2010. I considered an individual songbird patch faithful if it returned to, and established a territory in, the patch used for this study from one year to the next. I included each individual only once for analyses of patch fidelity decisions to ensure independence among samples.

I captured adults in mist-nets by placing nets in a bird's territory and attracted birds to nets by broadcasting vocalizations of white-eyed vireos recorded in the watershed and recordings of birds (eastern screech-owl [*Megascops asio*], western scrub-jay [*Aphelocoma californica*]) that vireos attempt to chase from their territory. After capturing each vireo, I recorded sex of each adult using their brood patch (females have a complete brood patch and males have a partial brood patch; Hopp et al. 1995), and placed colored bands on their legs with a unique color-band combination to enable identification of individuals with binoculars and during recapture.

I visited each territory twice per week to quantify the number and location of territories in the patch using visual and auditory observations (sensu Gregory et al. 2004; Kendeigh 1944). Upon detecting a white-eyed vireo, I followed the bird at a distance of about 10–20 m for about 30–60 min and recorded 3–5 locations of the individual with a minimum distance between locations of 20 m. I defined territories as locations where males defended an area or pairs remained for ≥1 month or attempted to nest. I relocated banded individuals by confirming color-band combinations with 2 independent observers or recapturing birds in mist-nets and mapped their territories during subsequent years to identify individuals exhibiting patch fidelity. Each year, I searched for banded individuals throughout the 100 ha patch of woodland to determine if individuals emigrated from the territory previously occupied. I recorded territory locations and locations of banded individuals with a GPS (global positioning system) and entered locations into ArcMap^{TM} 9.3 (ESRI$^{®}$, Redlands, CA) to record spatial data.

Number of fledglings

I searched for nests using behavioral cues (Campomizzi et al. 2009; Martin and Geupel 1993). Typically, I found nests by visually locating a bird I heard vocalizing, following a social pair, and then looking for behaviors that would lead to finding a nest such as an adult carrying nesting material or food, or returning to the nest to incubate eggs or brood nestlings. I visited each active nest every 3–4 days, a frequency to balance accurate monitoring of nest outcome while minimizing disturbance to nests, to monitor reproductive success for each territory. I counted the number of fledglings when possible in each territory. Because it was difficult to locate and obtain an accurate count of young fledglings, I primarily based the number of fledglings on the number of nestlings in a nest during the last visit to the nest prior to fledging. Basing the number of fledglings on the number of nestlings present during the last visit to a nest may bias the count high because partial predations could have occurred between the last visit to a nest and when young fledged. However, the potentially biased count would occur equally among all nests, not biasing one group of nests over another and thus, minimally impacting analyses. I addled brown-headed cowbird (*Molothrus ater*) eggs and removed cowbird young from nests to remove the impacts of brood parasitism because I have observed that cowbird nestlings typically kill white-eyed vireo nestlings. Adult vireos typically remove the dead white-eyed vireo nestlings, making collection of DNA from nestlings difficult.

Extra-pair paternity

I collected feather (2 secondaries) and blood samples (~10-25 ul) from adults and nestlings (Hoysak and Weatherhead 1991). I collected blood from adults by clipping a toe nail and collecting blood in a capillary tube (Sol et al. 2000) and from nestlings when they were about 3 days old by puncturing the tarso-metatarsal vein with a syringe (28–30 gauge) and collecting blood in a capillary tube (Bouwman et al. 2006; Manwell 1955). I kept feathers refrigerated and stored blood in lysis buffer (100 mM Tris-HCl pH8.0, 100 mM EDTA, 10 mM NaCl, 2% SDS) until lab analysis. For feathers, I cut the basal tip of the calamus into thin strips (Horváth et al. 2005; Rudnick et al. 2005). Strips of calamus and blood samples were incubated overnight in solution of protease K and lysis buffer at 55°C.

I extracted DNA using phenol-chloroform and precipitated DNA using ethanol (sensu Sambrook and Russell 2001; Appendix A). I amplified DNA using PCR at 6 microsatellite markers (Table 1) developed by Barr et al. (2007). PCR products were electrophoresed on an ABI Prism 3730XL sequencer (Applied Biosystems Inc.) and I manually interpreted resulting electopherographs with Genemarker (version 1.75, SoftGenetics LLC, State College, PA, USA) to identify and score alleles for each individual at each locus. I used program CERVUS (version 3.0.3; Kalinowski et al. 2007) to estimate non-exclusion probabilities for paternity and check for the presence of null alleles at each locus (Jones et al. 2010). Non-exclusion probability is the probability of not excluding an unrelated parent (Jones et al. 2010). A null allele is an allele at a microsatellite locus that PCR does not amplify to detectable levels (Dakin and Avise 2004).

I excluded a social parent as the genetic parent if offspring did not inherit one allele from that parent in a Mendelian manner and any discrepancy could not be accounted for by null alleles (Table A; Dakin and Avise 2004). I did not exclude social parents as genetic parents if either the social parent and or young were homozygous at a locus identified by CERVUS as having null alleles (null allele frequency estimate ≥0.2) and did not have an allele in common. For each nest, I first determined if the social female could be excluded as the mother and then determined if the social male could be excluded as the father.

Analysis

I expected males to use the number of fledglings in adjacent territories as an indicator of habitat quality regardless of paternity, thus I expected the probability of patch fidelity to be positively associated with the number of fledglings in adjacent territories. I used a logistic regression model (using the glm command in R) to predict the probability of patch fidelity for males, given the number of fledglings in adjacent territories. For this and subsequent models, I constructed the simplest model, with the fewest parameters that was biologically plausible, enabling analysis of the specific hypotheses of interest. I ran each model separately with data collected on either males or females. The model was:

(1) $logit(ptch\ fdlty) = \beta_0 + \beta_1 adj\ fldg$

where *ptch fdlty* was 0 if an individual did not exhibited patch fidelity and 1 if it did return. β_0 was the log odds of patch fidelity for an individual with no adjacent fledglings and β_1 was the change in log odds ratio for a 1 unit change in the number of fledglings in adjacent territories. *adj fldg* was the number of fledglings in adjacent territories. I tested the statistical null hypothesis $\beta_1 = 0$. For this and subsequent tests, I used $\alpha = 0.05$, considered the biological significance of the direction and slope of lines, and, for regression models, calculated Nagelkerke's R^2 to assess the proportion of explained variation (Nagelkerke 1991). I was interested in the biological significance of explanatory power of models and associations between variables, especially the direction and magnitude of the effect, rather than results of null hypothesis statistical tests (Cherry 1998; Johnson 1999). For this and subsequent tests, I considered an association to be biologically significant if probability of patch fidelity doubled or more, given the range of values for number of fledglings experienced by individuals in my study. Probability of patch fidelity (restricted to between 0.0–1.0) is unlikely to be near zero for any values because previous research has shown that some individuals return regardless of the number of fledglings in territories. Thus, a doubling of probability of patch fidelity is a substantial increase suggesting individuals may be making decisions based on the number of fledglings in territories. A doubling in probability of patch fidelity is also comparable to the effect size of percent of site fidelity in adults in experiments manipulating personal breeding success with a social mate (Haas 1998; Hoover 2003). I used R 2.11.1 (R Core Development Team 2010) for all statistical analyses and figures (annotated analysis code in Appendix B).

Male versus Female Patch Fidelity

I quantified patch fidelity, counted the number of fledglings in each territory, and identified the sex of each adult using the methods described above.

Analysis

I expected individual males and females to use the number of fledglings in adjacent territories as an indicator of habitat quality. I expected the probability of patch fidelity to increase with an increase in the number of fledglings in adjacent territories for both males and females. I used box-plots of data to compare the association between patch fidelity of males and females with the number of fledglings in adjacent territories. Next, I used logistic regression model 1 (above) to predict the probability of patch fidelity for females. I tested the statistical null hypothesis $\beta_1 = 0$ from model 1, considered the biological significance of the direction and slope of the lines, and Nagelkerke's R^2 for males and females.

Personal and Adjacent Fledglings

I quantified patch fidelity, counted the number of fledglings in each territory, and identified the sex of each adult using the methods described above.

Analysis

I investigated the association between patch fidelity of males and females, and the number of personal and adjacent fledglings. I tested if the number of personal and adjacent fledglings were correlated by visualizing the data using a scatter-plot and with Spearman's rank correlation (Zar 1999b) because data were not normally distributed. I expected the probability of patch fidelity of males and females to be more strongly, positively associated with the number of fledglings raised with a social mate than the number of fledglings in adjacent territories. Comparison of the strength of the association between probability of patch fidelity and number fledglings with a social mate versus number of fledglings in adjacent territories is qualitative, based on direction and slope of the lines, because the range of the number of fledglings was different for the 2 cases. I compared predictions of probability of patch fidelity for males and females based on logistic regression model 1 for the number of fledglings in adjacent territories and model 2 for the number of personal fledglings with a social mate:

$$(2)\ logit(ptch\ fdlty) = \beta_0 + \beta_1 prs\ fldg$$

where *ptch fdlty* was 0 if an individual did not exhibit patch fidelity and 1 if it did return. β_0 was the log odds of patch fidelity for an individual with no personal fledglings and β_1 was the change in log odds ratio for a 1 unit change in the number of personal fledglings. *prs fldg* was the number of personal fledglings. I tested the statistical null hypothesis $\beta_1 = 0$ for model 2, considered the biological significance of the direction and slope of the lines, and Nagelkerke's R^2 for males and females.

I expected individuals exhibiting patch fidelity to have been adjacent to territories with more fledglings the previous year than individuals that did not return. I expected this pattern to occur more strongly for individuals without personal fledglings. I considered an effect biologically significant if the median number of fledglings in adjacent territories was double the median of another group because it may suggest a mechanism used by individuals to make patch fidelity decisions. I explored the data using box-plots. Because sample sizes were small (10–22) and data not normally distributed, I used Fisher's exact tests (Zar 1999a) to determine if patch faithful individuals were adjacent to territories with more fledglings the previous year than individuals that did not show patch fidelity for males and females that did and did not fledge young with a social mate. I used 2 categories for the number of fledglings in adjacent territories, > or < the mean number of fledglings in adjacent territories (3.2) because Fisher's exact test uses categories, not continuous variables. I used 2-tailed tests even though I predicted a direction of the effect because effects could be in either direction, effects in either direction are ecologically interesting, and 2-tailed tests are more informative (Lombardi and Hurlbert 2009). The statistical null hypothesis for the first test was: males that fledged young with a social mate had the same proportion of patch faithful individuals that were adjacent to territories with > 3.2 fledglings as males that fledged young with a social mate, but did not show patch fidelity. The other 2 null hypotheses were similarly constructed for males without personal fledglings and females with personal fledglings. No females without personal fledglings exhibited patch fidelity, thus a statistical test was unnecessary.

3. RESULTS

I monitored white-eyed vireos in 27 territories in 2008 and 40 territories each year in 2009 and 2010. In those territories, I banded and collected tissue from 73 adults (50 males and 23 females) and 102 young from 36 nests. In 2009, 59% of males (n=22) and 50% of females (n=10) exhibited patch fidelity. In 2010, 44% of males (n=41) returned and 22% of females (n=18) exhibited patch fidelity.

I evaluated parentage for 102 young from 36 nests. I excluded the social male as the father of 3 of the 102 young and did not exclude any of the social females as the mother. Non-exclusion probability combined for all 6 loci was 0.00636 for the first parent (mother) and 0.00066 for the second parent (father; Table 1).

Male Patch Fidelity

The probability of patch fidelity for males without extra-pair paternity was positively associated with the number of fledglings in adjacent territories (Figure 1). However, I failed to reject the null hypothesis that $\beta_1 = 0$ ($\beta_1 = 0.166$, df = 35, $P = 0.247$) and the model did not explain variation in the data well (Nagelkerke's $R^2 = 0.054$).

Male versus Female Patch Fidelity

Median number of fledglings in adjacent territories the previous year was 60% higher for males and 62% higher for patch faithful females compared to number of fledglings adjacent to non-patch faithful males and females (Figure 2). The probability of patch fidelity increased similarly for males and females with an increase in the number of fledglings in adjacent territories (Figure 1). However, I failed to reject the null hypothesis that $\beta_1 = 0$ for males, as noted above, and for females ($\beta_1 = 0.121$, df = 17, P

= 0.670) and the model did not explain variation in the data well (Nagelkerke's R^2 =0.016).

Personal and Adjacent Fledglings

The number of personal fledglings raised with a social mate and the number of fledglings in adjacent territories were not correlated (S = 21895.28, n = 50, P = 0.723, r = –0.051). The probability of patch fidelity for males decreased with increasing number of young fledged with a social mate, whereas patch fidelity increased with increasing number of young fledged in adjacent territories (Figure 3). I failed to reject the null hypothesis that $\beta_1 = 0$ for the number of personal fledglings ($\beta_1 = –0.296$, df = 43, P = 0.360) and adjacent fledglings, as noted above, for predicting probability of patch fidelity in males. The model did not explain variation in the data well (Nagelkerke's R^2 = 0.029). The probability of patch fidelity for females increased with increasing number of young fledged with a social mate and with increasing number of young fledged in adjacent territories. I rejected the null hypothesis that $\beta_1 = 0$ for the number of personal fledglings for predicting probability of patch fidelity in females ($\beta_1 = 1.281$, df = 21, P = 0.048) and the model explained variation in the data well (Nagelkerke's R^2 = 0.409). I failed to reject the null hypothesis that $\beta_1 = 0$ for the relationship between probability of patch fidelity and number of fledglings in adjacent territories for females, as noted above.

Males with personal fledglings that exhibited patch fidelity were adjacent to territories with 133% more fledglings (or 5 individual fledglings) than males not showing patch fidelity (Figure 4). However, I failed to reject the null hypothesis (n = 11, *P* = 0.181). Males without personal fledglings that did not exhibited patch fidelity were adjacent to territories with 33% more fledglings (1 individual fledgling) than males showing patch fidelity (*n* = 22, *P* = 1.0; Figure 4). Females with personal fledglings that exhibited patch fidelity were adjacent to territories with 33% more fledglings (1 individual fledgling) than females not showing patch fidelity (*n* = 10, *P* = 0.571; Figure 4). No females without personal fledglings exhibited patch fidelity and those that did not showed patch fidelity were adjacent to territories with a median of 0 fledglings (Figure 4).

Table 1. Microsatellite markers used for parentage analysis, number of alleles at each marker, observed and expected heterozygosity (proportion of individuals in the population that were heterozygous at a specific locus), and null allele frequency estimate (an allele at a microsatellite locus that PCR does not amplify to detectable levels, calculated using an iterative algorithm based on observed and expected frequencies of various genotypes) from program CERVUS.

Microsatellite	No. of alleles	Observed heterozygosity	Expected heterozygosity	Null allele frequency estimate
BCV2-2	19	0.6282	0.8801	0.1657
BCV2-3	4	0.1387	0.3442	0.4232
BCV4-2	14	0.8868	0.8789	-0.0086
BCV4-5	14	0.8580	0.8712	0.0057
BCV4-6	3	0.1696	0.2467	0.2090
BCV5-1	59	0.5562	0.9733	0.2713

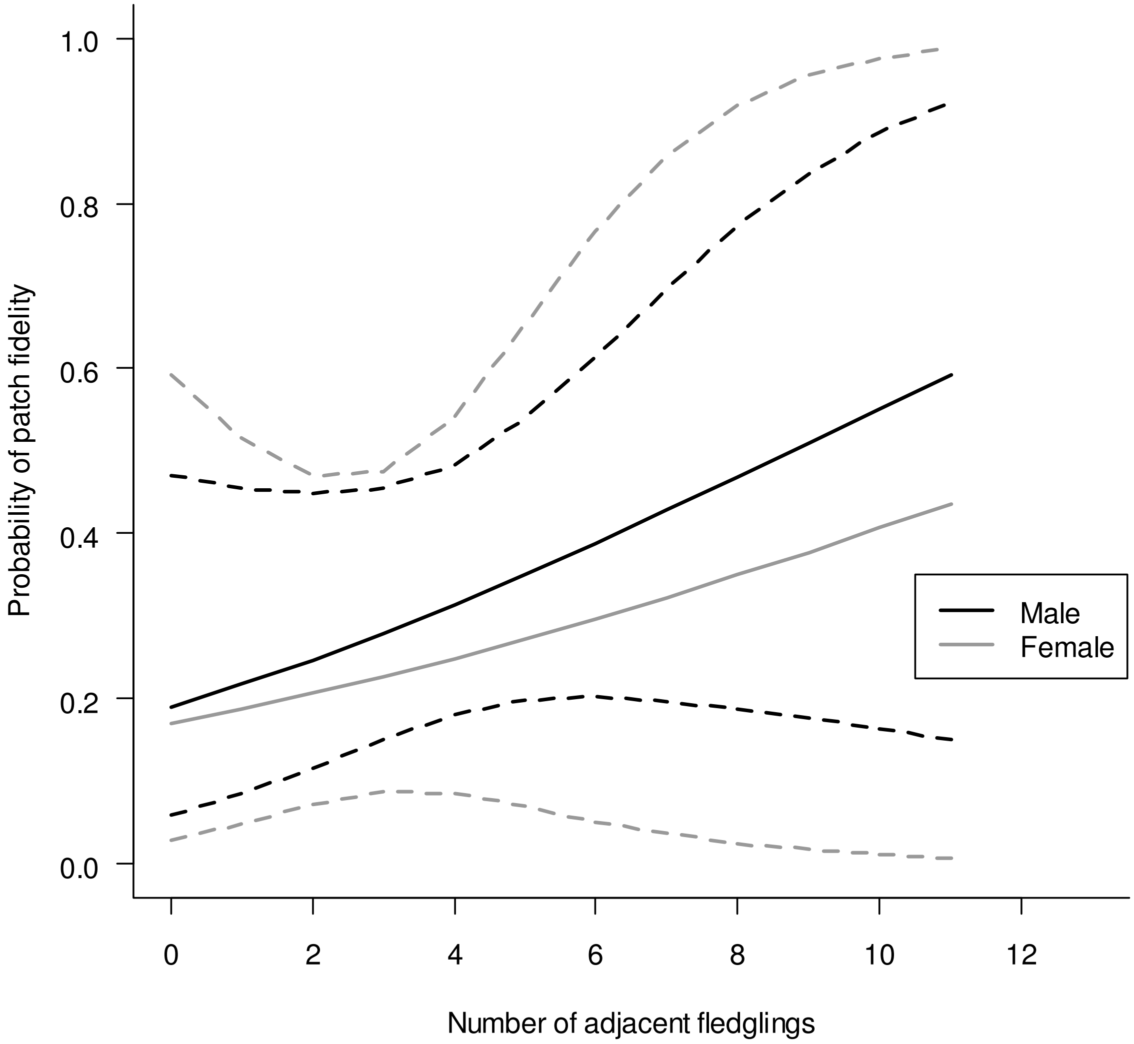

Figure 1. The probability of patch fidelity (solid lines) and 95% confidence limits (dashed lines) given the number of fledglings in adjacent territories for male and female white-eyed vireos in an oak juniper woodland in central Texas as predicted by logistic regression model 1.

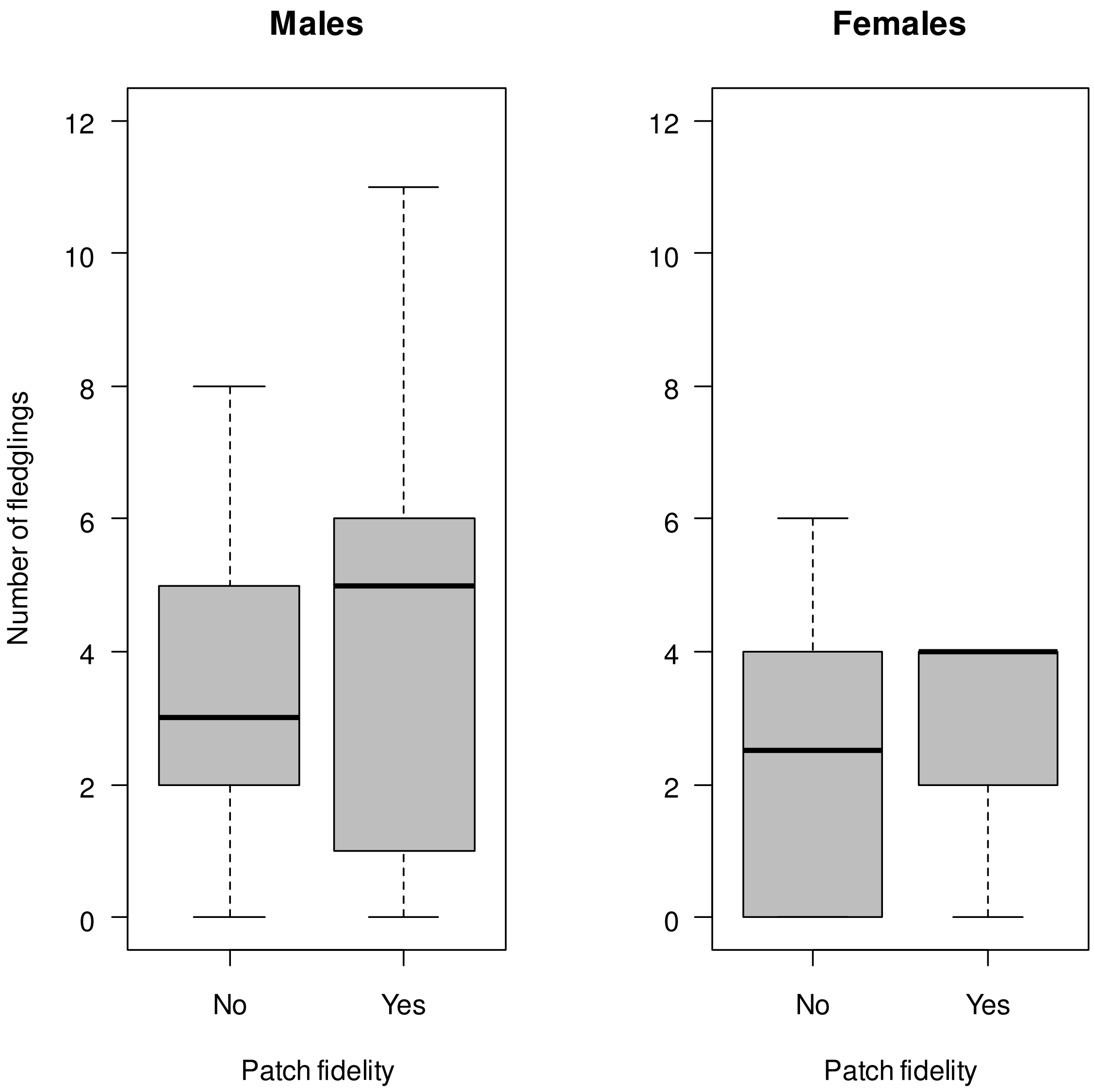

Figure 2. Box–plot of number of fledglings in adjacent territories for male (*n*=36) and female (*n*=18) white-eyed vireos that did and did not show patch fidelity from 2008–2009 or 2009–2010 in an oak-juniper woodland in central Texas. In each of the 4 boxplots, bold horizontal line is the median, edges of the box below and above the median are the 25th and 75th percentile, respectively, and whiskers extend to extent of the range.

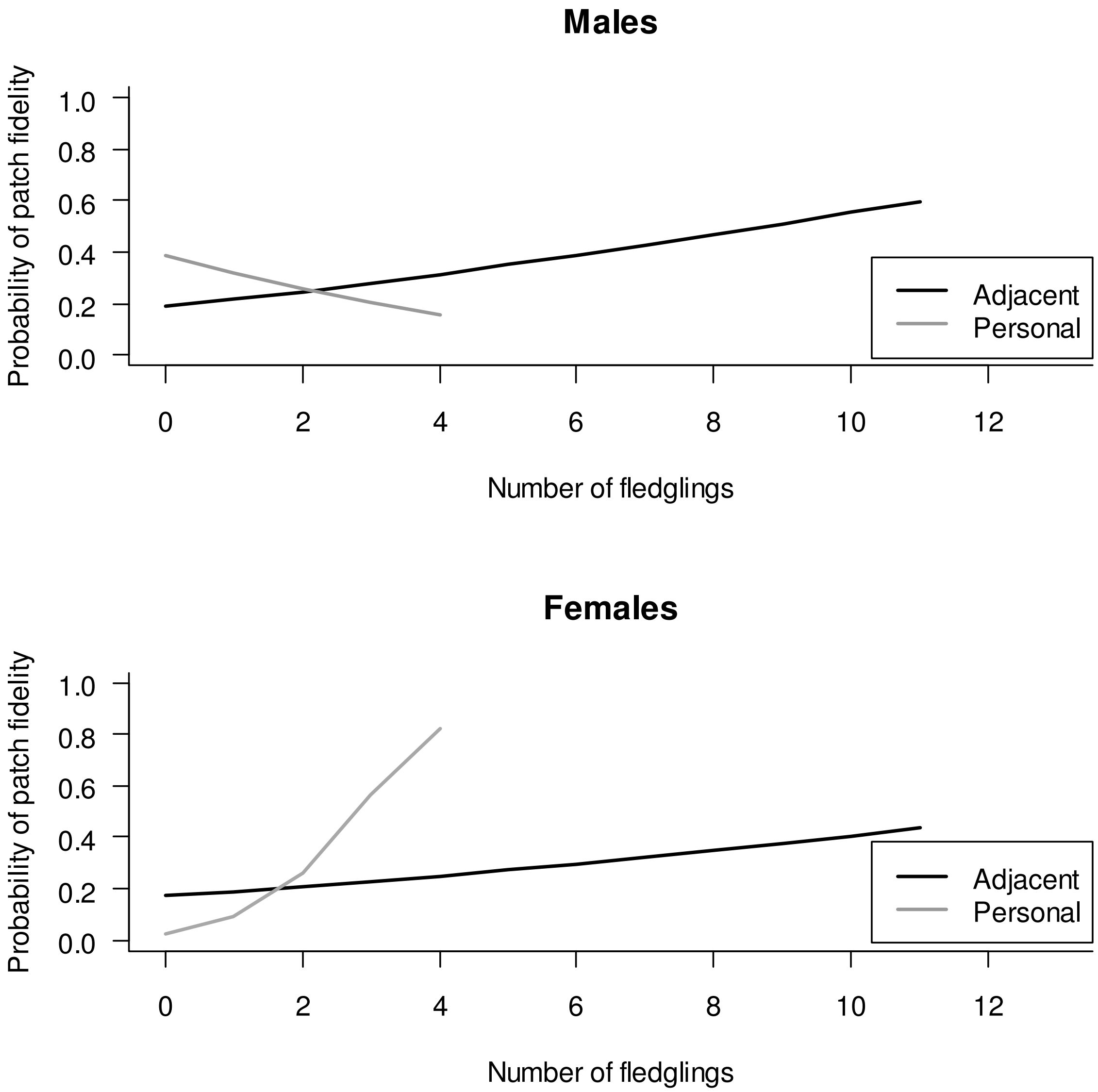

Figure 3. The probability of patch fidelity based on model predictions for male and female white-eyed vireos with different numbers of personal fledglings raised with a social mate and fledglings in adjacent territories. Predictions were based on model 1 for the number of fledglings in adjacent territories and model 2 for the number of fledglings with a social mate.

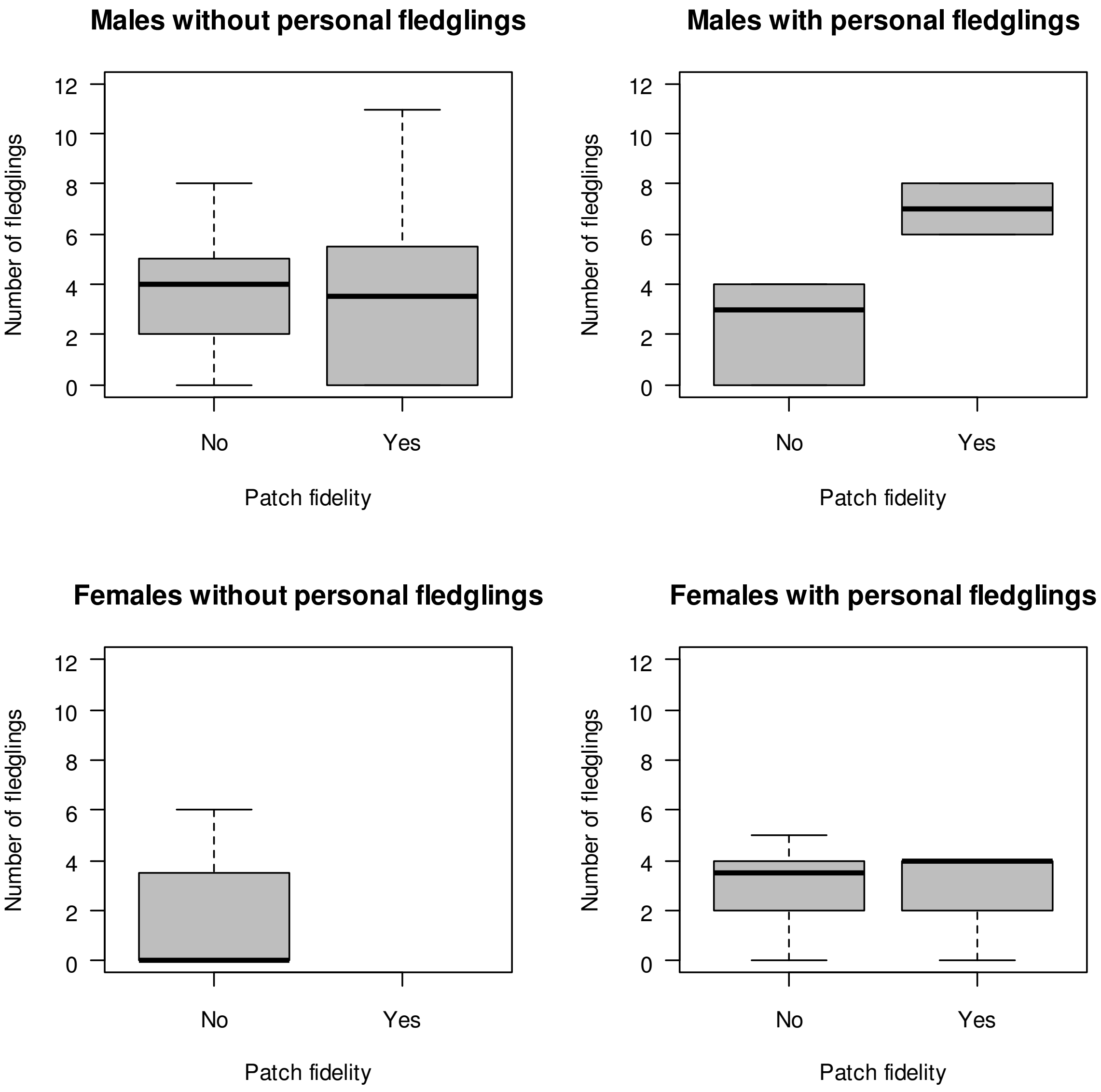

Figure 4. Box–plot of number of fledglings in adjacent territories for male (*n*=36) and female (*n*=18) white-eyed vireos with and without personal fledglings that did and did not show patch fidelity from 2008–2009 or 2009–2010 in an oak-juniper woodland in central Texas. In each of the 7 boxplots, the bold horizontal line is the median, the edges of the box below and above the median are the 25th and 75th percentile, respectively, and whiskers extend to extent of the range.

4. DISCUSSION

Male Patch Fidelity

My results do not support use of public information, measured as the number of fledglings in adjacent territories, as an important component in patch fidelity of males. Although my predictions from logistic regression models of probability of patch fidelity had a tendency toward a positive association with the number of fledglings in adjacent territories (Figure 1), the model did not explain variation in the data well. To my knowledge, this was the first test of the association between patch fidelity and number of nearby conspecific fledglings when frequency of extra-pair paternity was known. Because extra-pair paternity was low in this study, it is evidence that the use of public information may, to some extent, depend on extra-pair paternity. It is currently unknown if the association between probability of patch fidelity of males and number of fledglings in adjacent territories would differ depending on whether males had extra-pair copulations or extra-pair paternity in breeding systems with frequent cuckoldry. The number of fledglings in adjacent territories may influence male patch fidelity differently in systems with different frequencies of extra-pair copulations where paternity is obscured to some extent.

My results were inconsistent with a model of site fidelity indicating the importance of public information (Boulinier and Danchin 1997) and some field studies. The degree of temporal autocorrelation of habitat quality among years was important for previous model predictions of dispersal and site fidelity (Boulinier and Danchin 1997). Temporal autocorrelation of habitat quality is currently unknown in my study system. In a manipulative experiment, an association was found between number and body condition of offspring and immigration in collared flycatchers (*Ficedula albicollis*; Doligez et al. 2002). Similarly, frequency of male site fidelity was higher for males adjacent to territories that fledged young for prothonotary warblers (Hoover 2003) and in patches with higher density of young for bobolink (Dolichonyx oryzivorus; Bollinger and Gavin 1989). I am not aware of previous studies failing to find an association for male songbirds between site fidelity and reproductive performance of nearby conspecifics.

Although a larger sample size would likely enable rejection of the statistical null hypothesis ($\beta_1 = 0$) and effect size was large (probability of patch fidelity increased from 0.2 to 0.4 with a corresponding increase in number of adjacent fledglings from 0 to 6), 95% of the variation in the data were not explained by logistic regression model 1. These results suggest other reasons for patch fidelity may influence males more strongly than the number of fledglings in adjacent territories. Personal breeding success with a social mate (Schmidt 2004) was explored below as an explanation for patch fidelity in male white-eyed vireos. I discuss other possible explanations in the section on personal and adjacent fledglings below.

Male versus Female Patch Fidelity

My results do not support use of public information, measured as the number of fledglings in adjacent territories, as an important component in patch fidelity of males and females. Although predictions from logistic regression showed a positive relationship between number of fledglings in adjacent territories and probability of patch fidelity, the model failed to explain about 95% of variation in the data. As noted in the section above, these results are inconsistent with findings based on computer modeling and field studies examining the relationship between site fidelity and reproductive success of nearby conspecifics.

It was somewhat surprising that patch fidelity of males and females was not associated with the number of nearby conspecific fledglings considering some songbird species use cues from heterospecifics for habitat selection decisions (Forsman and Thomson 2008; Seppänen and Forsman 2007). Use of information from heterospecifics suggests direct fitness benefits are unnecessary for habitat selection decisions, yet I found no association with use of public information from conspecifics when extra-pair paternity was rare. Before conducting this research I assumed the number of heterospecific fledglings in nearby territories would influence patch fidelity decisions depending on overlap of resource use, phenology (Seppanen et al. 2007), and availability of information about conspecifics. It is possible, but unknown, if public information from heterospecifics was more important than information from conspecifics for patch fidelity decisions of white-eyed vireos in this study.

Although extra-pair paternity occurred rarely in this study, it is possible extra-pair copulations and extra-pair courting occurred and influenced patch fidelity of males and females. Adults may be unlikely to know if extra-territorial forays and extra-pair copulations resulted in fertilizations (Stutchbury et al. 2005), but these interactions may influence patch fidelity decisions. For example female site fidelity in hooded warblers (*Wilsonia citrina*) was associated with number of young of extra-pair paternity (Howlett and Stutchbury 2003). It is unknown if extra-territorial forays and extra-pair courting occurred frequently in this study and how the frequency of extra-pair paternity may influence associations between patch fidelity and the number of nearby conspecific fledglings.

Personal and Adjacent Fledglings

I hypothesized that probability of patch fidelity would be more strongly associated with the number of fledglings raised with a social mate than the number of fledglings in adjacent territories. Probability of patch fidelity of males showed a negative association with number of personal fledglings with a social mate (Figure 3). However, I failed to reject the statistical null hypothesis ($\beta_1 = 0$) and the model failed to explain about 95% of variation in the data, suggesting number of personal fledglings raised with a social mate was not important for patch fidelity decisions. These findings were inconsistent with some studies which found a positive association in some songbird species (Gavin and Bollinger 1988; Hoover 2003), but consistent with studies failing to find an association (Hallworth et al. 2008; Howlett and Stutchbury 2003; Sedgwick 2004). The lack of a positive association between probability of patch fidelity and number of personal fledglings was inconsistent with the win-stay lose-switch model of breeding site fidelity (Schmidt 2004). It is possible that basing patch fidelity decisions on number of young fledged with a social mate is not adaptive in some systems because of other factors in a male's territory or breeding patch that influence habitat quality among years, such as vegetation (Hallworth et al. 2008), presence of nest predators (Fontaine and Martin 2006), and food availability (Orians and Wittenberger 1991).

I hypothesized that individuals exhibiting patch fidelity had been adjacent to territories with more fledglings the previous year than individuals that did not return, especially for individuals without personal fledglings. I failed to reject the statistical null hypothesis, but interpret results cautiously because sample sizes were small. My results suggested males with and without personal fledglings with a social mate did not respond differently to the number of fledglings in adjacent territories. However, there was a threshold in the data for males with personal fledglings, below which all males did not exhibit patch fidelity and above which all males were patch faithful. I found that without personal breeding success, the number of fledglings in adjacent territories had little impact on a male's decision to return. Thus, the influence of the number of fledglings in adjacent territories on patch fidelity decisions by males may depend on the outcome of the male's breeding success with a social mate. Similar state-dependent processes have been observed in the context of foraging (Pompilio et al. 2006). Higher numbers of fledglings in adjacent territories may reinforce and strengthen a male's assessment of habitat quality when the male has successfully fledged young with a social mate. It is interesting that the number of fledglings in adjacent territories was similar for males without fledglings with a social mate that did and did not show patch fidelity because the number of adjacent fledglings may still accurately reflect habitat quality.

I found that both metrics I measured of public information and the win-stay lose-switch model failed to explain patch fidelity well for male white-eyed vireos in this study. This result was surprising because the win-stay lose-switch model was the dominant concept of why males show site fidelity. Similarly, I expected public information to explain patch fidelity well because of theoretical support (Danchin et al. 2004; Valone and Templeton 2002) and considering that the number of fledglings summarizes finer details of finding suitable mates, food supply, predator avoidance, availability of nest sites, etc.

Public information also seems useful considering frequency of reproductive success in one breeding season may be difficult for a songbird to assess within a single territory because nest predation was the primary cause of nest failure (Campomizzi et al. 2009) and was perhaps somewhat random within a patch of breeding habitat (Conkling 2010). Therefore, over time, natural selection may favor individuals using public information for patch fidelity decisions if there was indeed a fitness advantage to using this information. Perhaps some songbird species are not well adapted to perceive, interpret, and remember distributions of the number of con- and heterospecific fledglings over various spatial and temporal scales in breeding areas (Doligez et al. 2002).

My results suggest male white-eyed vireos use information not collected in this study for patch fidelity decisions. Males may use personal or public information unrelated to the number of fledglings. Individuals may gather information including food availability, predators, vegetation, inter- and intraspecific competition, body condition of offspring, and mate quality for making patch fidelity decisions. Males may gather information through prospecting behaviors during (Doligez et al. 2004; Pärt and Doligez 2003) and after the breeding season while on the breeding grounds (Ward 2005) or while selecting habitat during settlement of the next breeding season.

I hypothesized, and found support, that probability of patch fidelity of females increased more strongly with the number of fledglings raised with a social mate than with the number of fledglings in adjacent territories. I rejected the statistical null hypothesis ($\beta_1 = 0$), the trend suggested a potentially biologically relevant association, and the model explained about 41% of variation in the data. Results for female white-eyed vireos were consistent with the win-stay lose-switch model of site fidelity. A similar association, between personal reproductive success and site fidelity, was found for female willow flycatchers (*Empidonax traillii*; Sedgwick 2004).

I expected females exhibiting patch fidelity to have been adjacent to territories with more fledglings the previous year than individuals that did not return. I expected this pattern to occur more strongly for individuals without personal fledglings. I failed to reject the null hypothesis, but nevertheless found interesting patterns in the data. Females that did not fledge young with a social mate did not exhibit patch fidelity (Figure 4), again suggesting my results were consistent with the win-stay lose-switch model of site fidelity.

Perhaps personal reproductive success was more important than public information for females because individuals were unable to gather information on the number of fledglings in adjacent territories. It is possible females spent more time than males attending to nests and young. Although both sexes build nests, incubate eggs, and brood and feed young (Hopp et al. 1995), no data on time budgets is available. It is also possible that females have a stronger physiological response than males to nest predation, the most common cause of nest failure in this study. It is possible that for females, personal reproductive success with a social mate was more important for patch fidelity decisions than breeding success in neighboring territories because females did not adapt with the possibility of genetic offspring being raised in adjacent territories.

5. CONCLUSION

Overall, my results suggested patch fidelity of breeding white-eyed vireo males was not predicted well by the dominant concepts in ecology for predicting site fidelity (i.e., win-stay lose-switch model and public information). In contrast, patch fidelity of females was predicted well by the win-stay lose-switch model. To my knowledge, these are the first results showing no association between patch fidelity and reproductive success of nearby conspecifics. It is important to note that extra-pair paternity was infrequent in this study and unmeasured in other studies of public information and habitat selection. My results suggested future research may be useful for investigating factors in the environment, besides number of fledglings, for predicting patch fidelity of males. Future research is also needed to determine how patch fidelity decisions based on personal and public information influence patch and population level persistence of species.

My results may suggest some characteristics of breeding areas helpful for conservation of songbirds, although different songbird species may show different patterns than I found here. Conditions in the patch of woodland and in adjacent grasslands included multiple anthropogenic land-uses including grazing in and around the woodland, hunting, adjacent rural residential buildings, county roads, and power lines. Maintaining high levels of nest success is important to ensure the return of females to areas managed for breeding songbirds because female patch fidelity was associated with personal reproductive success with a social mate. High levels of nest success will also ensure young are produced for maintaining populations. Ensuring the return of males is less certain because male patch fidelity was not associated with the number of fledglings raised with a social mate or the number of fledglings in adjacent territories. However, about half of females and males exhibited patch fidelity, suggesting compatibility with ongoing land-use. These results suggest that maintaining large patches of woodland within human-altered landscapes may enable males and females to return to breeding patches regardless of the reasons for patch fidelity. For preserving a patch of woodland for breeding white-eyed vireos, it appears the status quo may be sufficient for this species.

REFERENCES

Ahlering MA, Faaborg J. 2006. Avian habitat management meets conspecific attraction: if you build it, will they come? Auk. 123:301–312.

Arlt D, Part T. 2007. Nonideal breeding habitat selection: a mismatch between preference and fitness. Ecology. 88:792–801.

Barr KR, Dharmarajan G, Rhodes OE, Lance RL, Leberg PL. 2007. Novel microsatellite loci for the study of the black-capped vireo (*Vireo atricapillus*). Mol Ecol Notes. 7:1067–1069.

Betts MG, Hadley AS, Rodenhouse N, Nocera JJ. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. Proc R Soc Lond B Biol Sci. 275:2257–2263.

Bollinger EK, Gavin TA. 1989. The effects of site quality on breeding-site ridelity in bobolinks. Auk. 106:584-594.

Bollinger EK, Gavin TA. 1991. Patterns of extra-pair fertilizations in bobolinks. Behav Ecol Sociobiol. 29:1–7.

Bonnie KE, Earley RL. 2007. Expanding the scope for social information use. Anim Behav. 74:171–181.

Boulinier T, Danchin E. 1997. The use of conspecific reproductive success for breeding patch selection in terrestrial migratory species. Evol Ecol. 11:505–517.

Bouwman KM, Burke T, Komdeur J. 2006. How female reed buntings benefit from extra-pair mating behaviour: testing hypotheses through patterns of paternity in sequential broods. Mol Ecol. 15:2589–2600.

Campomizzi AJ, Morrison ML, Farrell SL, Wilkins RN, Drees BM, Packard JM. 2009. Red imported fire ants can decrease songbird nest survival. Condor. 111:534–537.

Cherry S. 1998. Statistical tests in publications of The Wildlife Society. Wildl Soc Bull. 26:947–953.

Conkling TJ. 2010. Analysis of the black-capped vireo and white-eyed vireo nest predator assemblages [Master's Thesis]. College Station: Texas A&M University.

Dakin EE, Avise JC. 2004. Microsatellite null alleles in parentage analysis. Heredity. 93:504–509.

Dall SRX, Giraldeau L-A, Olsson O, McNamara JM, Stephens DW. 2005. Information and its use by animals in evolutionary ecology. Trends Ecol Evol. 20:187–193.

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

Danchin E, Heg D, Doligez B. 2001. Public information and breeding habitat selection. In: Clobert J, Danchin E, Dhondt AA, Nichols JD, editors. Dispersal. New York: Oxford University Press. p. 243–258.

Doligez B, Cadet C, Danchin E, Boulinier T. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. Anim Behav. 66:973–988.

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

Doligez B, Part T, Danchin E. 2004. Prospecting in the collared flycatcher: gathering public information for future breeding habitat selection? Anim Behav. 67:457–466.

Fletcher RJ. 2007. Species interactions and population density mediate the use of social cues for habitat selection. J Anim Ecol. 76:598–606.

Fontaine JJ, Martin TE. 2006. Habitat selection responses of parents to offspring predation risk: an experimental test. Am Nat. 168:811–818.

Forsman JT, Thomson RL. 2008. Evidence of information collection from heterospecifics in cavity-nesting birds. Ibis. 150:409–412.

Fretwell SD, Lucas Jr. HL. 1969. On territorial behavior and other factors influencing habitat distribution in birds. Acta Biotheor. 19:16–52.

Gavin TA, Bollinger EK. 1988. Reproductive correlates of breeding-site fidelity in bobolinks (*Dolichonyx oryzivorus*). Ecology. 69:96–103.

Gould SJ, Lewontin RC. 1979. The spandrels of San Marco and the Panglossian paradigm: a critique of the adaptationist programme. Proc R Soc Lond B Biol Sci. 205:581–598.

Greenwood PJ, Harvey PH. 1982. The natal and breeding dispersal of birds. Annu Rev Ecol Syst. 13:1–21.

Gregory RD, Gibbons DW, Donald PF. 2004. Bird census and survey techniques. In: Sutherland WJ, Newton I, Green RE, editors. Bird ecology and conservation: a handbook of techniques. New York, NY, USA: Oxford University Press Inc. p. 17–52.

Griffith SC, Owens IPF, Thuman KA. 2002. Extra pair paternity in birds: a review of interspecific variation and adaptive function. Mol Ecol. 11:2195–2212.

Haas CA. 1998. Effects of prior nesting success on site fidelity and breeding dispersal: an experimental approach. Auk. 115:929–936.

Hallworth M, Ueland A, Anderson E, Lambert JD, Reitsma L. 2008. Habitat selection and site fidelity of Canada warblers (*Wilsonia canadensis*) in central New Hampshire. Auk. 125:880–888.

Hilden O. 1965. Habitat selection in birds. Ann Zool Fenn. 2:53–75.

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

Hopp SL, Kirby A, Boone CA. 1995. White-eyed vireo (*Vireo griseus*). In: Poole A editor. The Birds of North America Online 168. Ithaca: Cornell Lab of Ornithology.

Horváth MB, Martínez-Cruz B, Negro JJ, Kalmár L, Godoy JA. 2005. An overlooked DNA source for non-invasive genetic analysis in birds. J Avian Biol. 36:84–88.

Howlett JS, Stutchbury BJM. 2003. Determinants of between-season site, territory , and mate fidelity in hooded warblers (*Wilsonia citrina*). Auk. 120:457–465.

Hoysak DJ, Weatherhead PJ. 1991. Sampling blood from birds: a technique and an assessment of its effect. Condor. 93:746–752.

Johnson DH. 1999. The insignificance of statistical significance testing. J Wildl Manage. 63:763–772.

Jones AG, Small CM, Paczolt KA, Ratterman NL. 2010. A practical guide to methods of parentage analysis. Mol Ecol Resources. 10:6–30.

Jones J. 2001. Habitat selection studies in avian ecology: a critical review. Auk. 118:557–562.

Kalinowski ST, Taper ML, Marshall TC. 2007. Revising how the computer program CERVUS accommodates genotyping error increases success in paternity assignment. Mol Ecol. 16:1099–1106.

Kendeigh SC. 1944. Measurement of bird populations. Ecol Monogr. 14:67–106.

Klopfer PH, Ganzhorn JU. 1985. Habitat selection: behavioral aspects. In: Cody ML, editor. Habitat selection in birds. Orlando, FL: Academic Press, Inc. p. 435–453.

Lombardi CM, Hurlbert SH. 2009. Misprescription and misuse of one-tailed tests. Austral Ecol. 34:447-468.

Manwell RD. 1955. The blood protozoa of seventeen species of sparrows and other fringillidae. J Eukaryot Microbiol. 2:21–27.

Martin TE. 1993. Nest predation and nest sites - new perspectives on old patterns. Bioscience. 43:523–532.

Martin TE, Geupel GR. 1993. Nest-monitoring plots: methods for locating nests and monitoring success. J Field Ornithol. 64:507–519.

Misenhelter MD, Rotenberry JT. 2000. Choices and consequences of habitat occupancy and nest site selection in sage sparrows. Ecology. 81:2892–2901.

Møller AP. 2000. Male parental care, female reproductive success, and extrapair paternity. Behav Ecol. 11:161–168.

Morton ES, Stutchbury BJM, Howlett JS, Piper WH. 1998. Genetic monogamy in blue-headed vireos and a comparison with a sympatric vireo with extrapair paternity. Behav Ecol. 9:515–524.

Nagelkerke NJD. 1991. A note on a general definition of the coefficient of determination. Biometrika. 78:691–692.

National Oceanic and Atmospheric Administration's National Weather Service (NOAA). 2011. Waco climatology home page. http://www.srh.noaa.gov/fwd/?n=actclimo. Date accessed 01 February 2011.

Neudorf DL, Stutchbury BJM, Piper WH. 1997. Covert extraterritorial behavior of female hooded warblers. Behav Ecol. 8:595–600.

Nocera JJ, Betts MG. 2010. The role of social information in avian habitat selection. Condor. 112:222–224.

Orians GH, Wittenberger JF. 1991. Spatial and temporal scales in habitat selection. Am Nat. 137:S29–S49.

Parejo D, Danchin E, Aviles JM. 2004. The heterospecific habitat copying hypothesis: can competitors indicate habitat quality? Behav Ecol. 16:96–105.

Pärt T, Doligez B. 2003. Gathering public information for habitat selection: prospecting birds cue on parental activity. Proc R Soc Lond B Biol Sci. 270:1809–1813.

Petit LJ, Petit DR. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell-Lucas models. Ecol Monogr. 66:367–387.

Pompilio L, Kacelnik A, Behmer ST. 2006. State-dependent learned valuation drives choice in an invertebrate. Science. 311:1613–1615.

R Core Development Team. 2010. R: a language and environment for statistical computing. Vienna, Austria: R Foundation for Statistical Computing; [cited 2010 December 15]. Available from: http://www.r-project.org.

Rudnick JA, Katzner TE, Bragin EA, Rhodes OE, Dewoody JA. 2005. Using naturally shed feathers for individual identification, genetic parentage analyses, and population monitoring in an endangered Eastern imperial eagle (*Aquila heliaca*) population from Kazakhstan. Mol Ecol. 14:2959–2967.

Sambrook J, Russell DW. 2001. Molecular cloning, a laboratory manual, Third ed. Cold Spring Harbor, New York: Cold Spring Harbor Laboratory Press.

Schmidt KA. 2001. Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. Evol Ecol Res. 3:633–648.

Schmidt KA. 2004. Site fidelity in temporally correlated environments enhances population persistence. Ecol Lett. 7:176–184.

Sedgwick JA. 2004. Site fidelity, territory fidelity, and natal philopatry in willow flycatchers (*Empidonax trailii*). Auk. 121:1103–1121.

Seppänen J-T, Forsman JT. 2007. Interspecific social learning: novel preference can be acquired from a competing species. Curr Biol. 17:1248–1252.

Seppanen J-T, Forsman JT, Monkkonen M, Thomson RL. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. Ecology. 88:1622–1633.

Sol D, Jovani R, Torres J. 2000. Geographical variation in blood parasites in feral pigeons: the role of vectors. Ecography. 23:307–314.

Stutchbury BJM. 1998. Extra-pair mating effort of male hooded warblers, *Wilsonia citrina*. Anim Behav. 55:553–561.

Stutchbury BJM, Pitcher TE, Norris DR, Tuttle EM, Gonser RA. 2005. Does male extra-territory foray effort affect fertilization success in hooded warblers *Wilsonia citrina*? J Avian Biol. 36:471–477.

Switzer PV. 1993. Site fidelity in predictable and unpredictable habitats. Evol Ecol. 7:533–555.

Valone TJ, Templeton JJ. 2002. Public information for the sssessment of quality: a widespread social phenomenon. Philos Trans R Soc Lond B Biol Sci. 357:1549–1557.

Ward MP. 2005. Habitat selection by dispersing yellow-headed blackbirds: evidence of prospecting and the use of public information. Oecologia. 145:650–657.

Webster MS, Chuang-Dobbs HC, Holmes RT. 2001. Microsatellite identification of extrapair sires in a socially monogamous warbler. Behav Ecol. 12:439–446.

Yom-Tov Y. 2001. An updated list and some comments on the occurrence of intraspecific nest parasitism in birds. Ibis. 143:133–143.

Zar JH. 1999a. More on dichotomous variables. Biostatistical analysis. Fourth ed. Upper Saddle River, NJ: Prentice–Hall, Inc. p. 516–570.

Zar JH. 1999b. Simple linear correlation. Biostatistical analysis. Fourth ed. Upper Saddle River, NJ: Prentice–Hall, Inc. p. 377–412.

APPENDIX A

DNA EXTRACTION METHODS

For Feather Samples

1. With scissors, cut tip of feather up to beginning of barbs.
2. Add 350 µL SNET.
3. Add 20 µL ProK.
4. Incubate at 55 C overnight.
5. Add 92.5 µL potassium acetate, invert 20 sec.
6. Incubate on ice for 5 min.
7. Centrifuge at maximum for 3 min at 0 C.
8. Add 44.3 µL 3M sodium acetate, ph 5.2 (1/10 vol).
9. Add 15.0 µL 1M $MgCl2$ (final concentration 0.01 M).
10. Invert 20 sec.
11. Add 1,004.0 µL ethanol (ice cold, 95%, 2 vol).
12. Invert 10 sec.
13. Incubate in freezer 1 hr.
14. Centrifuge at maximum speed for 35 min at 0 C.
15. Gently pour off liquid.
16. Add 100 µL ethanol (ice cold, 70%).
17. Centrifuge at maximum speed for 10 min.
18. Gently pour off liquid.
19. Add 100 µL ethanol (ice cold, 70%).
20. Centrifuge at maximum speed for 10 min.
21. Gently pour off liquid.
22. Incubate at room temperature for 10 min with top open.
23. Add 35 µL TLE.
24. Refrigerate.
25. Check DNA concentration on nanodrop.
26. Dilute DNA to 35 ng/µL with TLE.

For blood samples

1. Gently invert blood sample in lysis buffer.
2. Use 780 µL blood in lysis buffer
3. Add 20 µL ProK (10mg/mL)
4. Incubate overnight at 55 C and rotation.
5. Add 800 µL PCI (1 volume, room temperature)
6. Invert for 20 sec
7. Centrifuge at max rpm for 5 min at 4 C.
8. Collect and save supernatant (top layer) with p200 pipet, 50 µL at a time.
9. Add 550 µL CI (1 volume, room temperature).
10. Invert for 20 sec.
11. Centrifuge at max rpm for 5 min at 4 C.

12. Collect and save supernatant (top layer) with p200 pipet, 50 µL at a time.
13. Add 800 µL 100% ethanol (2 volumes, ice cold).
14. Invert 10 sec.
15. Incubate at 4 C for 1 hr.
16. Centrifuge at max rpm for 15 min at 4 C (hinge side of tube facing away from center).
17. Gently pour off liquid (look for pellet on hinge side, near bottom of tube).
18. Add 100 µL ethanol (70%, ice cold)
19. Invert 5 sec.
20. Centrifuge at max rpm for 10 min at 4 C (hinge side out).
21. Gently pour off liquid, looking for and saving pellet.
22. Repeat 70% ethanol rinse a second time.
23. Leave tube open, upside down for 10 min at room temp.
24. Add 35 µL TLE.
25. Flick tube for 20 sec.
26. Incubate for 5 min at room temp.
27. Use pipet to rnse hinge side of tube with its own TLE 7 to 8 times.
28. Refrigerate.
29. Check DNA concentration on nanodrop.
30. Dilute DNA concentration to 35 ng/µL with TLE.

APPENDIX B

R CODE USED FOR ANALYSES

```
##########################################################################
#analysis for revision of dissertation after defense
##########################################################################
#use all data
#set working directory
setwd("D:/PhD_Work/Analysis/Data/")
#load data
fidelity.data1=read.table("Site_Fidelity_Paternity_2010.11.08.txt", header=TRUE,
colClasses=c("factor", "factor", "numeric", "factor", "numeric"))
#check structure of data
str(fidelity.data1)
##########################################################################
#check correlations between predictor variables
#plot histograms
hist(fidelity.data1$personal.fledglings)
hist(fidelity.data1$neighbor.fledglings)
#plot scatterplot
plot(fidelity.data1$personal.fledglings, fidelity.data1$neighbor.fledglings)
#test for correlation using spearman's test
cor.test(fidelity.data1$personal.fledglings, fidelity.data1$neighbor.fledglings,
alternative="two.sided", method = "spearman")
##########################################################################
#exploratory plots of data
#boxplot of number of fledglings in adjacent territories by patch fidelity yes, no
boxplot(fidelity.data1$neighbor.fledglings ~ fidelity.data1$patch.fidelity)
#subset data for individuals that showed patch fidelity
sub.sf1=subset(fidelity.data1, fidelity.data1$patch.fidelity==1)
#subset data for individuals not showing patch fidelity
sub.no.sf1=subset(fidelity.data1, fidelity.data1$patch.fidelity==0)
#create plotting space with 1 row and 2 columns
par(mfrow=c(2, 1))
#plot histograms of number of fledglings in adjacent territories for individuals that did
#and did not show patch fidelity
hist(sub.sf1$neighbor.fledglings, xlim=c(0, 12), ylim=c(0, 10))
hist(sub.no.sf1$neighbor.fledglings, xlim=c(0, 12), ylim=c(0, 10))
#plot data for males
#subset data for males
sub.m=subset(fidelity.data1, fidelity.data1$sex==0)
#check structure of data
str(sub.m)
```

```
#boxplot of number of fledglings in adjacent territories for males and females that did
and did not show patch fidelity
#plot males
par(mfrow=c(1, 2))
boxplot(sub.m$neighbor.fledglings ~ sub.m$patch.fidelity, bty="l", las=1, col="gray",
main="Males", ylim=c(0, 12), xlab="Patch fidelity", names = c("No", "Yes"),
ylab="Number of fledglings")
#plot females
#subset data for females
sub.f=subset(fidelity.data1, fidelity.data1$sex==1)
#check structure of data
str(sub.f)
boxplot(sub.f$neighbor.fledglings ~ sub.f$patch.fidelity, bty="l", las=1, col="gray",
main="Females", ylim=c(0, 12), xlab="Patch fidelity", names = c("No", "Yes"),
ylab="")
#plot histogram of number of fledglings in adjacent territories for males that did and did
#not show patch fidelity
#subset data for males showing patch fidelity
sub.sf.m=subset(sub.m, sub.m$patch.fidelity==1)
#subset data for males not showing patch fidelity
sub.no.sf.m=subset(sub.m, sub.m$patch.fidelity==0)
#check structure of data
str(sub.sf.m)
str(sub.no.sf.m)
#create plotting space with 1 row and 2 columns
par(mfrow=c(2, 1))
hist(sub.sf.m$neighbor.fledglings, xlim=c(0, 12), ylim=c(0, 10))
hist(sub.no.sf.m$neighbor.fledglings, xlim=c(0, 12), ylim=c(0, 10))
##########################################################################
#objective 1 for males
#run glm for males, association between number of fledglings in adjacent territories and
#probability of patch fidelity
glm1.m=glm(formula=patch.fidelity ~ 1 + neighbor.fledglings, data=sub.m,
family=binomial(link="logit"))
#look at output for fitted glm1 model
summary(glm1.m)
#make values for predictor variable
fledg.num=seq(0, 11, 1)
#make prediction of probability of patch fidelity with no fledglings for males
plogis.predict1m=plogis(coef(summary(glm1.m))[1,1] +
coef(summary(glm1.m))[2,1]*fledg.num)
#plot prediction of probability of patch fidelity for values of number of neighboring
fledglings
```

```
plot(fledg.num, plogis.predict1m, type="l", lwd=2, las=1, bty="l", xlim=c(0, 13),
ylim=c(0.0, 1.0), xlab="Number of adjacent fledglings", ylab="Probability of patch
fidelity")
#add 95% Confidence intervals
#attach data
attach(sub.m)
#make data frame for values for range of prediction
fledge.num.df=data.frame(neighbor.fledglings=fledg.num)
#predict
predict.cl1m=predict(glm1.m, fledge.num.df, interval=("confidence"), level=0.95,
type="link", se.fit=TRUE)
#calculate 95% confidence intervals
upper.cl1m=predict.cl1m$fit + 1.96 * predict.cl1m$se.fit
lower.cl1m=predict.cl1m$fit - 1.96 * predict.cl1m$se.fit
#transform confidence intervals onto logit scale
logit.upper.cl1m=plogis(upper.cl1m)
logit.lower.cl1m=plogis(lower.cl1m)
lines(fledg.num, logit.upper.cl1m, type = "l", lty="dashed", lwd=2)
lines(fledg.num, logit.lower.cl1m, type = "l", lty="dashed", lwd=2)
#detach data
detach(sub.m)
############################################
#calculate r squared
library(fmsb)
NagelkerkeR2(glm1.m)
############################################
#test if median number of fledglings in adjacent territories are equal to each other for
#males the did and did not show patch fidelity
wilcox.test(sub.sf.m$neighbor.fledglings, sub.no.sf.m$neighbor.fledglings, alternative =
"two.sided", mu = 0, paired = FALSE, exact = NULL, correct = TRUE, conf.int =
FALSE, conf.level = 0.95)
##################################################################
#objective 2 for females
#run glm for females, association between number of fledglings in adjacent territories
#and probability of patch fidelity
glm1.f=glm(formula=patch.fidelity ~ 1 + neighbor.fledglings, data=sub.f,
family=binomial(link="logit"))
summary(glm1.f)
#make values for predictor variable
fledg.num=seq(0, 11, 1)
#make prediction of probability of patch fidelity with no fledglings for males
plogis.predict1f=plogis(coef(summary(glm1.f))[1,1] +
coef(summary(glm1.f))[2,1]*fledg.num)
```

```
#plot prediction of probability of patch fidelity for values of number of neighboring
#fledglings
lines(fledg.num, plogis.predict1f, type="l", lwd=2, col="gray60")
#add 95% Confidence intervals
#attach data
attach(sub.f)
#make data frame for values for range of prediction
fledge.num.df=data.frame(neighbor.fledglings=fledg.num)
#predict
predict.cl1f=predict(glm1.f, fledge.num.df, interval=("confidence"), level=0.95,
type="link", se.fit=TRUE)
#calculate 95% confidence intervals
upper.cl1f=predict.cl1f$fit + 1.96 * predict.cl1f$se.fit
lower.cl1f=predict.cl1f$fit - 1.96 * predict.cl1f$se.fit
#transform confidence intervals onto logit scale
logit.upper.cl1f=plogis(upper.cl1f)
logit.lower.cl1f=plogis(lower.cl1f)
lines(fledg.num, logit.upper.cl1f, type = "l", lty="dashed", lwd=2, col="gray60")
lines(fledg.num, logit.lower.cl1f, type = "l", lty="dashed", lwd=2, col="gray60")
#add legend
legend(10.5, 0.35, legend = c("Male", "Female"), col = c("black", "gray60"),lwd = 2)
#detach data
detach(sub.f)
##################################
#calculate r squared
NagelkerkeR2(glm1.f)
##################################
#######################################################
#objective 3 for males
#run glm for males, association between number of personal fledglings and probability
#of patch fidelity
glm2.m=glm(formula=patch.fidelity ~ 1 + as.numeric(personal.fledglings), data=sub.m,
family=binomial(link="logit"))
summary(glm2.m)
#make prediction of probability of patch fidelity based on number of personal fledglings
#for males
pers.fledg.num=seq(0, 4, 1)
plogis.predict2m=plogis(coef(summary(glm2.m))[1,1] +
coef(summary(glm2.m))[2,1]*pers.fledg.num)
#plot result for probability of patch fidelity for number of adjacent fledglings
par(mfrow=c(2, 1))
plot(fledg.num, plogis.predict1m, type="l", lwd=2, las=1, bty="l", xlim=c(0, 13),
ylim=c(0.0, 1.0), main="Males", xlab="Number of fledglings", ylab="Probability of
patch fidelity")
```

```
#plot result for probability of patch fidelity for number of personal fledglings
lines(pers.fledg.num, plogis.predict2m, type="l", col="gray60", lwd=2)
#add legend
legend(10.3, 0.38, legend = c("Adjacent", "Personal"), col = c("black", "gray60"),lwd =
2)
####################################
#calculate r squared
NagelkerkeR2(glm2.m)
####################################
#objective 3 for females
#run glm for females, association between number of personal fledglings and probability
#of patch fidelity
glm2.f=glm(formula=patch.fidelity ~ 1 + as.numeric(personal.fledglings), data=sub.f,
family=binomial(link="logit"))
summary(glm2.f)
#make prediction of probability of patch fidelity based on number of personal fledglings
#for females
pers.fledg.num=seq(0, 4, 1)
plogis.predict2f=plogis(coef(summary(glm2.f))[1,1] +
coef(summary(glm2.f))[2,1]*pers.fledg.num)
#plot result for probability of patch fidelity for number of adjacent fledglings
plot(fledg.num, plogis.predict1f, type="l", lwd=2, las=1, bty="l", xlim=c(0, 13),
ylim=c(0.0, 1.0), main="Females", xlab="Number of fledglings", ylab="Probability of
patch fidelity")
#plot result for probability of patch fidelity for number of personal fledglings
lines(pers.fledg.num, plogis.predict2f, type="l", col="gray66", lwd=2)
#add legend
legend(10.3, 0.38, legend = c("Adjacent", "Personal"), col = c("black", "gray60"),lwd =
2)
####################################
#calculate r squared
NagelkerkeR2(glm2.f)
####################################
##########################################################
#second part of objective 3
#load data with 0 for no personal fledglings, 1 for personal fledglings
fidelity.data2=read.table("Site_Fidelity_Paternity_2010.11.08pers.txt", header=TRUE,
colClasses=c("factor", "factor", "factor", "factor", "numeric"))
str(fidelity.data2)
#plot boxplot for number of fledglings in adjacent territories for males and females with
#and without personal fledglings and that did and did not show site fidelity
boxplot(fidelity.data2$neighbor.fledglings ~ fidelity.data2$sex ~
fidelity.data2$personal.fledglings)
#subset data
```

```
#males without personal fledglings
sub.m2=subset(fidelity.data2, sex==0)
sub.m2.nofl=subset(sub.m2, personal.fledglings==0)
#males with personal fledglings
sub.m2.fl=subset(sub.m2, personal.fledglings==1)
#boxplot for males
par(mfrow=c(2, 2))
boxplot(sub.m2.nofl$neighbor.fledglings ~ sub.m2.nofl$patch.fidelity, las=1, ylim=c(0,
12), col="gray", main="Males without personal fledglings", xlab="Patch fidelity",
names = c("No", "Yes"), ylab="Number of fledglings")
boxplot(sub.m2.fl$neighbor.fledglings ~ sub.m2.fl$patch.fidelity, las=1, ylim=c(0, 12),
col="gray", main="Males with personal fledglings", xlab="Patch fidelity", names =
c("No", "Yes"), ylab="Number of fledglings")
#subset data for females
sub.f2=subset(fidelity.data2, sex==1)
sub.f2.nofl=subset(sub.f2, personal.fledglings==0)
sub.f2.fl=subset(sub.f2, personal.fledglings==1)
#boxplots for females
boxplot(sub.f2.nofl$neighbor.fledglings ~ sub.f2.nofl$patch.fidelity, las=1, ylim=c(0,
12), col="gray", main="Females without personal fledglings", xlab="Patch fidelity",
names = c("No", "Yes"), ylab="Number of fledglings")
boxplot(sub.f2.fl$neighbor.fledglings ~ sub.f2.fl$patch.fidelity, las=1, ylim=c(0, 12),
col="gray", main="Females with personal fledglings", xlab="Patch fidelity", names =
c("No", "Yes"), ylab="Number of fledglings")
######################################
#use fisher's exact test to test if individuals that fledged young with a social mate had the
#same proportion of patch faithful individuals that were adjacent to territories with > 3.2
#(the mean) fledglings as males that fledged young with a social mate, but did not show
#patch fidelity
#males with personal fledglings
m.flg=matrix(c(2, 0, 3, 6), nrow=2, ncol=2, byrow=TRUE)
fisher.m.flg=fisher.test(m.flg, alternative = "two.sided")
fisher.m.flg
###############
#males without personal fledglings
m.no.flg=matrix(c(5, 4, 10, 6), nrow=2, ncol=2, byrow=TRUE)
fisher.m.no.flg=fisher.test(m.no.flg, alternative = "two.sided")
fisher.m.no.flg
###############
#females with fledglings
f.flg=matrix(c(3, 1, 3, 3), nrow=2, ncol=2, byrow=TRUE)
fisher.f.flg=fisher.test(f.flg, alternative = "two.sided")
fisher.f.flg
##############
```

```
#females without fledglings
f.no.flg=matrix(c(0, 0, 2, 5), nrow=2, ncol=2, byrow=TRUE)
fisher.f.no.flg=fisher.test(f.no.flg, alternative = "two.sided")
fisher.f.no.flg
#######################################################################
#end of analysis!
#######################################################################
```

VITA

Name: Andrew James Campomizzi

Address: 210 Nagle Hall, Department of Wildlife and Fisheries Sciences, Texas
A&M University College Station, TX 77843-2258.

Email Address: acampomizzi@tamu.edu

Education: B.S., Biology, University of Dayton, 1999
M.S., Wildlife and Fisheries Sciences, Texas A&M University, 2008
Ph.D., Wildlife and Fisheries Sciences, Texas A&M University, 2011