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Win-stay, lose-switch and public information strategies for patch fidelity of songbirds with rare extra-pair paternity

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Determining where organisms breed and understanding why they breed in particular locations are fundamental biological questions with conservation implications. Breeding-site fidelity is common in migratory, territorial songbirds and is typically thought to occur following reproductive success with a social mate and success of nearby conspecifics. It is currently unknown if frequency of extra-pair paternity in a population influences use of information about reproductive success of nearby conspecifics for site fidelity decisions. We investigated patch fidelity of white-eyed vireos (*Vireo griseus*) based on reproductive success and quantified frequency of extra-pair paternity. We found support only for females making patch fidelity decisions following reproductive success with a social mate. Patch fidelity of males was not associated with reproductive success of nearby conspecifics, suggesting males may not use this information when extra-pair paternity is infrequent or the association is non-existent in this species.

D etermining where organisms breed and understanding why they breed in particular locations are basic biological questions with conservation implications. Studies of habitat selection in migratory, territorial songbirds that have focused on associations with vegetative or other habitat metrics often ignore that many individuals simply return to breed in the same location as the previous year (i.e., breeding site fidelity). Songbirds can use various information to make breeding site fidelity decisions. The two conceptual models posited in the literature for making site fidelity decisions are the win-stay, lose-switch strategy[1] and what we call the public information strategy[2].

Most research on breeding site fidelity in migratory songbirds has focused on understanding the role of reproductive success with a social mate[3–6]. Number of offspring is a measure of reproductive success resulting partially from physical and biological conditions of a breeding site and thus indicates habitat quality[2,7]. The win-stay, lose-switch strategy predicts an adult will exhibit site fidelity (stay) when able to produce offspring with a social mate, but disperse (switch) to other sites for subsequent breeding attempts when unable to produce offspring. This strategy enables adults to maximize the number of offspring produced over their lifetime if habitat quality is temporally auto-correlated among years[1,8]. Some empirical studies of breeding site fidelity support the win-stay, lose-switch strategy for females only[9] or for both males and females[3–5,10]. However, about 20 to 50% of individuals exhibit site fidelity even when unsuccessful in producing offspring with a social mate[3,4,6].

Other researchers suggested the public information strategy as an alternative for deciding site fidelity. Public information, in general, is information acquired vicariously and indicates performance of individuals producing observable cues[11]. Particular to site fidelity, the public information strategy predicts adults should exhibit site fidelity if nearby conspecifics had reproductive success, particularly in patchy environments when habitat quality is temporally auto-correlated among years[2]. Thus, an individual may exhibit site fidelity even if it failed to successfully reproduce with a social mate because public information indicates good habitat quality based on number of offspring in neighboring territories[6,11–13]. For example, Hoover[4] found that for reproductively 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.

Previous research has not addressed the possibility that frequency of extra-pair paternity in a population may play a role in use of the public information strategy. Researchers have implicitly assumed that if a male responds

positively to reproductive success in neighboring territories, the male is assessing habitat quality only. However, males may be assessing reproductive success in adjacent territories because it provides a partial assessment of their own reproductive success through extra-pair paternity. What researchers previously thought was the public information strategy actually could be information about an individual's reproductive success and thus, essentially an extension of the win-stay, lose-switch strategy[4]. Extra-pair paternity is common among neighboring territories[14–17] in many songbird species[18]. Collared flycatchers (*Ficedula albicollis*) used the public information strategy for site fidelity decisions[12] and can have frequent extra-pair paternity, with 33% of nests having young of extra-pair paternity[18]. Similarly, black-throated blue-warblers (*Dendroica caerulescens*) used public information for habitat selection[19] and can have young of extra pair paternity in 34% of nests[18]. To our knowledge, no study has quantified frequency of extra-pair paternity in studies of male use of the public information strategy. Thus, it is currently unknown if individuals using reproductive success of neighbors for site fidelity decisions in systems with frequent extra-pair paternity are truly following the public information strategy in which reproductive success of neighbors indicates habitat quality, or if they are assessing their own extended reproductive success through extra-pair paternity.

An association between patch fidelity and number of offspring in nearby territories in a species with rare extra-pair paternity enables distinction between use of the public information strategy for assessing habitat quality or use of information about extended reproductive success through extra-pair paternity. Alternatively, an association between patch fidelity and number of adjacent offspring in a system with frequent extra-pair paternity fails to enable distinction between two reasons information about adjacent fledglings may be used. In systems with frequent extra-pair paternity, use of the public information strategy by females versus males can provide a means to distinguish whether public information is an indication of habitat quality or reproductive success through extra-pair paternity. Females cannot have reproductive success in adjacent territories through extra-pair paternity, but can through conspecific, brood parasitism. However, frequency of conspecific brood parasitism in females is rare compared with extra-pair paternity in males[20]. Thus, if females use presence of offspring in adjacent territories for site fidelity decisions, it is likely they are assessing habitat quality, not their own reproductive success through conspecific brood parasitism.

We investigated ability of the win-stay, lose-switch and public information strategies to explain patch fidelity of white-eyed vireos (*Vireo griseus*). Frequency of extra-pair paternity was unknown in this species. We expected extra-pair paternity to be rare because breeding is asynchronous[21] due to frequent nest failure and subsequent re-nesting[22,23], and a high level of paternal care[24,25]. We chose white-eyed vireos for our study because much is known about their breeding biology[24], nests are accessible within 2 m of the ground, adults can be captured and marked, and microsatellite markers were available for assessing parentage[26]. Our objective was not to test many predictor variables (e.g., vegetation) to determine which might be associated with patch fidelity. Rather, our objectives were to (1) test the public information strategy by evaluating the importance of number of offspring in adjacent territories for making patch fidelity decisions, (2) test the win-stay, lose-switch strategy by evaluating importance of number of offspring with a social mate for patch fidelity decisions, (3) compare the two strategies for making patch fidelity decisions, and (4) quantify frequency of extra-pair paternity for interpreting results of the public information strategy.

Results

We monitored white-eyed vireos in 27 territories in 2008, 40 territories in 2009, and 40 territories in 2010. Forty-one percent of territories produced offspring in 2008 and 28% in 2009. In 2009, 59% of males ($n = 22$) and 50% of females ($n = 10$) exhibited patch fidelity.

In 2010, 44% of males ($n = 41$) and 22% of females ($n = 18$) exhibited patch fidelity. From the monitored territories, we banded and collected tissue from 50 adults (33 males and 17 females) and 102 young from 36 nests, which we used for statistical and parentage analyses.

Public information. Median number of offspring in adjacent territories was 4, both for males that did and did not show patch fidelity (Fig. 1). Median number of offspring in adjacent territories was 4 for females that showed patch fidelity and 2.5 for those that did not (Fig. 1). Our logistic regression model for patch fidelity of males with a parameter for number of offspring in adjacent territories was unsupported ($\Delta AIC_c = 2.033$) compared to the intercept-only model which provided the best fit (Table 1). For females, the model with a parameter for number of adjacent offspring was also unsupported ($\Delta AIC_c = 5.785$) compared to the model with a parameter for number of offspring with a social mate, which was the best-fit model (Table 1).

Win-stay, lose-switch. Median number of offspring with a social mate was 0 both for males that did and did not exhibit patch fidelity. Median number of offspring with a social mate was 2 for patch faithful females and 0.5 for females that were not patch faithful. Number of offspring with a social mate and number of offspring in adjacent territories were uncorrelated ($S = 22801.86$, $n = 50$, $P = 0.51$, $r = -0.095$). The model for patch fidelity with a parameter for number of offspring with a social mate was unsupported for males ($\Delta AIC_c = 0.582$) compared to the intercept-only model (Table 1). The model with a parameter for number of offspring with a social mate was the best-fit model for females ($\Delta AIC_c = 0.0$; Table 1). Predicted patch fidelity from the best model for females showed probability of patch fidelity increased with increasing number of offspring with a social mate (Fig. 2). We did not estimate predicted patch fidelity of males because the best-fit model was the intercept-only model for neither strategy of patch fidelity.

Extra-pair paternity. Our study population was more genetically diverse than most avian populations[27] (Table 2), providing a powerful suite of markers for parentage inference. Non-exclusion probability combined for all six loci was 0.00636 for the first parent (mother) and 0.00066 for the second parent (father). Non-exclusion probability combined for the three loci without null alleles was 0.06239 for the mother and 0.01501 for the father. Extra-pair paternity was infrequent; we excluded the social male as the father for 2 of the 102 offspring and failed to exclude any social females as the mother.

Discussion

Overall, patch fidelity of breeding white-eyed vireo males and females was inconsistent with the public information strategy. Patch fidelity of females, but not males, was consistent with the win-stay, lose-switch strategy. Our results were inconsistent with previous field studies supporting the public information strategy. For example, Doligez et al.[12] found that manipulating number of offspring influenced emigration in collared flycatchers because local conspecifics collected and decided site fidelity, in part, based on public information. Similarly, frequency of male site fidelity was higher for males adjacent to territories that produced offspring for prothonotary warblers[4] and in breeding patches with higher density of young for bobolink (*Dolichonyx oryzivorus*)[6]. We are unaware of previous field studies failing to find support for reproductive success of nearby conspecifics being important for site fidelity of male songbirds.

Our results suggest male patch fidelity decisions were influenced by factors other than number of offspring in adjacent territories. For instance, we are unaware how frequently extra-pair copulations and courting occurred that failed to result in extra-pair offspring. Adults,
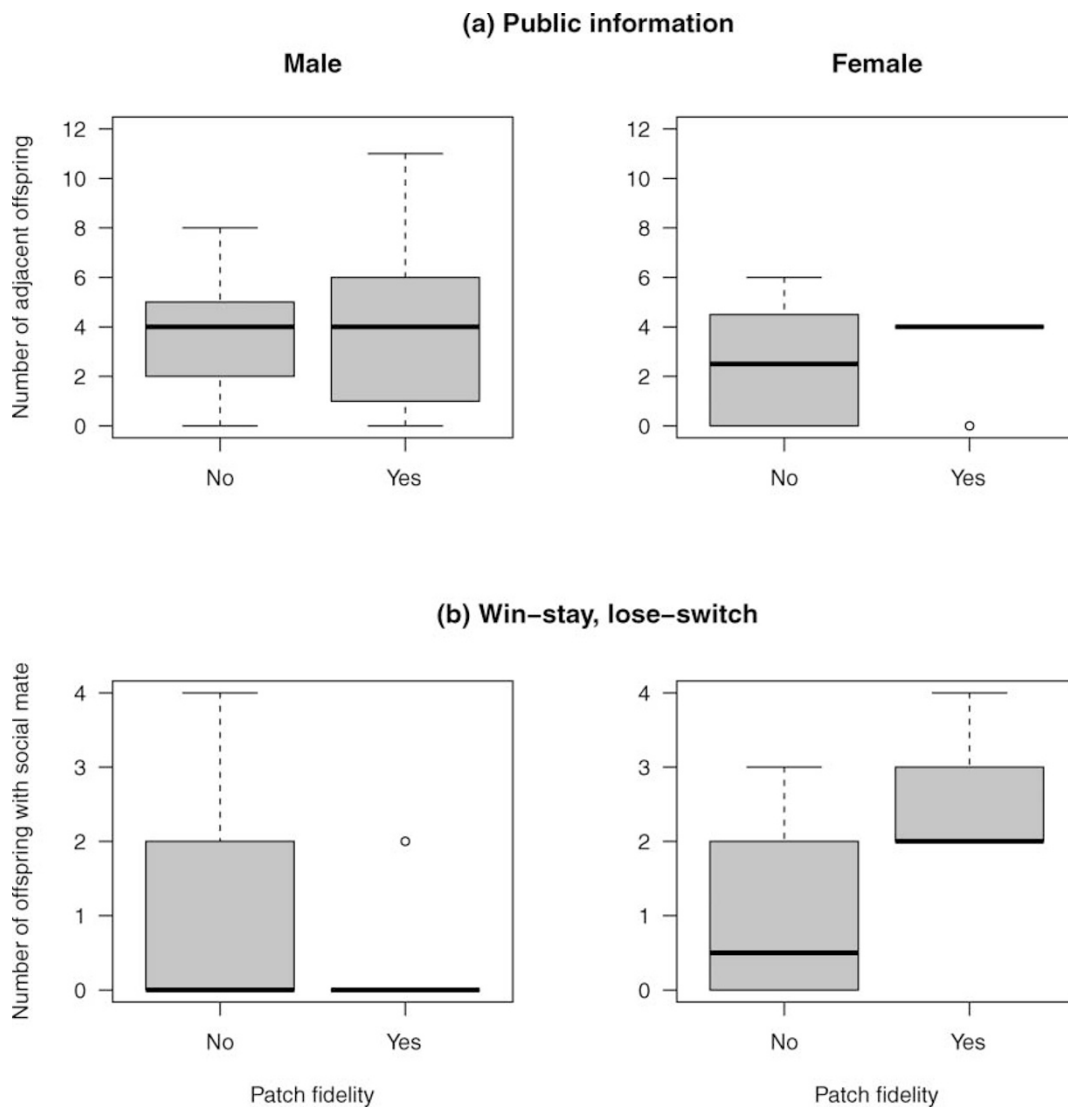
Figure 1 | Box-plot of number of offspring (a) in adjacent territories (indicative of the public information strategy) of male and female white-eyed vireos that did and did not show breeding patch fidelity and (b) with a social mate (indicative of the win-stay, lose-switch strategy) for males and females that did and did not show patch fidelity.

particularly males, may be unlikely to know if extra-territorial forays and extra-pair copulations result in fertilizations[28], 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[29], indicating that extra-pair interactions influenced female site fidelity rather than total number of offspring. Additionally, mate fidelity, although common in some breeding systems, was rare, occurring for only one pair, and therefore likely unimportant for patch fidelity in our study.

Extra-pair paternity was infrequent and thus, did not confer information about reproductive success through extra-pair copulations. The public information strategy failed to predict patch fidelity well, suggesting males may not have used this strategy because it did not provide information about reproductive success. It is possible male white-eyed vireos simply do not use the public information strategy, regardless of frequency of extra-pair paternity. Results for females were inconsistent with using the public information strategy simply because the strategy enables adults to show patch fidelity based on habitat quality. Future research may determine when the public information strategy is likely to be used by males for site fidelity decisions under various frequencies of extra-pair paternity. To our knowledge, this was the first test of the association between

patch fidelity and number of nearby conspecific offspring when frequency of extra-pair paternity was known.

Male patch fidelity was inconsistent with the win-stay, lose-switch strategy, based on number of offspring with a social mate (Table 1). Some studies found a positive association between reproductive success with a social mate and site fidelity[4,10], which is consistent with the win-stay, lose-switch strategy. Our results, however, were consistent with studies that also failed to find an association[9,29,30], suggesting the win-stay, lose-switch strategy is not always supported. For females, the model for the win-stay, lose-switch strategy was supported. We found a positive association between patch fidelity and number of offspring with a social mate. In previous research, a positive association between personal reproductive success and site fidelity was found for female willow flycatchers (*Empidonax traillii*)[9]. Personal reproductive success with a social mate may be more important for patch fidelity decisions than breeding success in neighboring territories because females did not evolve with the possibility of offspring being raised in adjacent territories. Additionally, females may be less able to gather public information by prospecting. 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[24], no data on time budgets is available.

Table 1 | Evaluation of logistic regression models for predicting patch fidelity of male and female white-eyed vireos based on number of adjacent, conspecific offspring or offspring with a social mate. K is the number of parameters in each model. *n* = 33 for males and 17 for females

Conceptual model	Variables in model	K	AIC$_c$	ΔAIC$_c$	w_i	Deviance
	Males					
Public information	Adjacent offspring	2	47.424	2.033	0.172	43.024
Win-stay, lose-switch	Personal offspring	2	45.973	0.582	0.354	41.573
Neither strategy	Intercept only	1	45.391	0.0	0.474	43.262
	Females					
Public information	Adjacent offspring	2	25.117	5.785	0.045	20.260
Win-stay, lose-switch	Personal offspring	2	19.332	0.0	0.815	14.475
Neither strategy	Intercept only	1	22.864	3.532	0.139	20.597

Our results were surprising because the win-stay, lose-switch strategy is the dominant concept for why male songbirds show site fidelity. Similarly, we expected the public information strategy to explain patch fidelity well because of theoretical and empirical support[11,31], and because number of offspring summarizes finer details of finding suitable mates, food availability, predator avoidance, and availability of nest sites. Basing patch fidelity decisions on number of offspring produced may be maladaptive in some systems because of other factors in a territory or breeding patch that may not be temporally auto-correlated and influence habitat quality among years. Such factors include vegetation[30], presence of nest predators[32], food availability[33], inter- and intraspecific competition, and body condition of offspring and mates. Males may gather public information through prospecting behaviors during[34,35] and after the breeding season while on the breeding grounds[36] or while selecting habitat during settlement of the next breeding season. Additionally, information from heterospecifics, such as co-occurring songbirds, may play a role in patch fidelity decisions depending on overlap of resource use, phenology[37], and availability of information about conspecifics. If use of conspecific public information depends on frequency of extra-pair paternity, then use of public information from heterospecifics is enigmatic because information from heterospecifics cannot reflect an individual's reproductive success through extra-pair paternity.

Our results suggest future research investigating factors besides number of conspecific fledglings for predicting patch fidelity of males may be useful. Future research would also be useful to determine how patch fidelity decisions based on the win-stay, lose-switch and public information strategies influence patch and population level persistence of species.

Methods

Study species and area. We studied white-eyed vireos nesting in a 100 ha patch of mature, oak-juniper (*Quercus-Juniperus*) woodland in the Leon River watershed in Coryell County, in central Texas, USA. We attempted to monitor all nesting white-eyed vireos in a 60 ha focal area and searched throughout the 100 ha patch for individuals exhibiting patch fidelity. White-eyed vireos are neotropical migrants that breed in the eastern half of the U.S. from March to August[24]. They are one of the most common songbirds in woodlands and shrublands in the ~400,000 ha Leon River watershed. White-eyed vireos can immigrate to and emigrate from patches of woodland within and among years suggesting behavioral patterns at our study site should not be unique. Nest predation is the primary cause of nest failure in white-eyed vireos in the study area[22,23] and has shown weak associations with vegetation characteristics[23].

Patch fidelity. We conducted fieldwork from March to July of 2008 to 2010. We captured adults in mist-nets by broadcasting various avian vocalizations, recorded sex of each adult based on brood patch[24], and used unique leg color-band combinations to enable identification of individuals with binoculars. To determine number and location of territories, we censused the 60 ha focal area twice per week and conducted territory mapping[38,39]. We recorded locations of individuals using a hand-held GPS (global positioning system) and entered locations into ArcMap™ 9.3 (ESRI®, Redlands, CA). Territories were locations where males defended an area or pairs remained for ≥1 month or attempted to nest. We relocated banded individuals by confirming color-band combinations with two independent observers or by recapturing birds.

We recorded patch fidelity of adults from 2008 to 2009 and 2009 to 2010. An adult exhibited patch fidelity if it established a territory in the study patch in consecutive years. We used patch rather than territory fidelity because we were interested if individuals returned to the patch based on conspecific reproductive success in adjacent territories as an indicator of habitat quality in the area. Also, data on territory and patch fidelity were essentially the same. Only one male and one female exhibited patch fidelity, but did not return to the same or adjacent territory. As with all site fidelity studies of small, vagile songbirds, we were unable to distinguish between dispersal from the patch and mortality[3,4,6].

Number of offspring. We recorded number of offspring by counting number of fledglings in territories in 2008 and 2009. We found nests using behavioral cues and systematic searching[40]. To monitor reproductive success for each territory, we visited each active nest every three to four days, on expected fledge date, and each subsequent day until young fledged or the nest failed. We counted number of fledglings when possible in each territory, but primarily based counts on number of nestlings during the last visit to nests prior to fledging because it is difficult to locate and obtain an accurate count of fledglings. This approach may bias counts high because partial nest predations could have occurred between the last visit to a nest and when young fledged. However, potentially biased counts would likely occur equally among all nests. We were not always able to capture and band both social parents. We were only able to assign the number of offspring to social parents if adults were banded, thus in some cases the number of offspring could only be assigned to one parent. We addled brown-headed cowbird (*Molothrus ater*) eggs and removed cowbird young from nests to remove impacts of brood parasitism because we have observed cowbird nestlings causing mortality of white-eyed vireo nestlings.

Extra-pair paternity. We collected 10 to 25 ul of blood by clipping a toe nail in adults[41] and from the tarso-metatarsal vein in nestlings with a syringe[42,43]. We also collected feathers (two secondaries) from adults and nestlings[44]. We 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, we cut the basal tip of calamus into thin strips[45,46]. Strips of calamus and blood samples were rotated overnight in a solution of proteinase K and lysis buffer at 55°C.

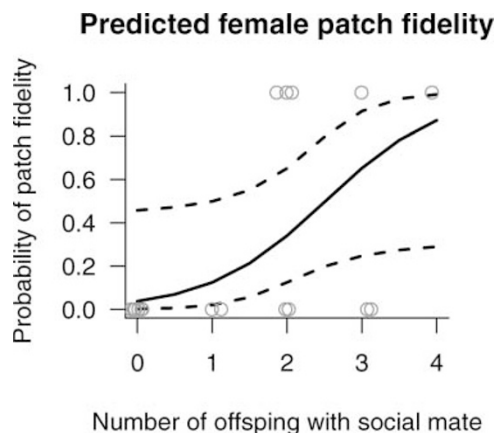## Predicted female patch fidelity

Figure 2 | Probability of patch fidelity for females given number of offspring with a social mate, based on the best-fit logistic regression model, which included a parameter for observed number of offspring with a social mate for the win-stay, lose-switch strategy. Predictions for males are not shown because the best-fit model was the intercept-only model for neither strategy of patch fidelity.

Table 2 | Microsatellite loci used for parentage analysis, number of alleles at each locus, observed and expected heterozygosity, and null allele frequency estimate from program CERVUS

Microsatellite	Alleles	Observed heterozygosity	Expected heterozygosity	Null allele frequency
BCV2-2	19	0.63	0.88	0.17
BCV2-3	4	0.14	0.34	0.42
BCV4-2	14	0.89	0.88	-0.01
BCV4-5	14	0.86	0.87	0.01
BCV4-6	3	0.17	0.25	0.21
BCV5-1	59	0.56	0.97	0.27

We extracted DNA using phenol-chloroform, precipitated DNA using ethanol[47], and amplified DNA using PCR at six microsatellite loci developed by Barr et al.[26]. PCR products were electrophoresed using an ABI Prism 3730XL sequencer (Applied Biosystems Inc.) and we manually interpreted resulting electropherograms with Genemarker (version 1.75, SoftGenetics LLC, State College) to score alleles. We estimated non-exclusion probabilities (i.e., probability of not excluding an unrelated parent) for parents and checked for presence of null alleles using program CERVUS[48–50]. We excluded a social parent as genetic parent if offspring did not inherit one allele from that parent at each locus in a Mendelian manner and any discrepancy could not be accounted for by null alleles[50]. We did not exclude social parents as genetic parents if either the social parent or young were homozygous at a locus with null alleles (null allele frequency estimate $\geq$ 0.2) and did not have an allele in common. For each offspring, we 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. We used box-plots to visualize data and logistic regression models to predict probability of patch fidelity given number of offspring[51]. Although a combination of number of offspring with a social mate, number of offspring in adjacent territories, and many other variables may influence patch fidelity, our specific goal was to test existing conceptual models of patch fidelity strategies[1,31]. Based on the theoretical models of patch fidelity, our win-stay, lose-switch strategy model regressed patch fidelity based on number of offspring with a social mate whereas the public information strategy regressed patch fidelity based on number of offspring in adjacent territories. We ran each model separately for males and females because each sex may respond differently to number of offspring. Due to modest sample size, we were unable to adequately fit an increased parameter model that treated adults as a random effect. Rather, we included each adult only once for analyses of patch fidelity to ensure independence among samples, randomly selecting patch fidelity data from 2009 or 2010 for individuals monitored both years.

We expected number of offspring in adjacent territories to be used by individuals as an indicator of habitat quality and thus, to be a good predictor of patch fidelity. We also expected number of offspring with a social mate to be a good predictor of patch fidelity. We tested if number of offspring with a social mate and number of adjacent offspring were correlated by graphing data using a scatter-plot and with Spearman's rank correlation because data were not normally distributed[52]. We defined adjacent territories as those sharing a geographic boundary. The logistic regression model was $logit(patch\ fidelity_i) = \beta_0 + \beta_1 x_i$. $patch\ fidelity_i$ was one if an adult exhibited patch fidelity and zero if it did not. β_0 was log odds of patch fidelity for an individual with either no adjacent offspring (public information strategy) or no offspring with a social mate (win-stay, lose-switch strategy) and β_1 was change in log odds ratio for a one unit change in number of fledglings. x_i was either number of offspring in adjacent territories or number of offspring with a social mate.

We used AIC$_c$ model selection (Akaike Information Criterion corrected for small sample size relative to number of parameters in the model)[53] to determine whether models supported either strategy for each sex relative to an intercept-only model indicating neither strategy was used[54]. We also evaluated biological significance of direction and magnitude of effects[55,56]. We used R 2.14.0[57] for all statistical analyses and figures (annotated analysis code available in supplementary information).

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Author contributions

All authors conceived of the project and reviewed the manuscript. AJC and SLF conducted fieldwork. AJC and JAD conducted lab work. AJC analyzed the data and wrote the main manuscript text.

Additional information