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Why come back home? Investigating the proximate factors that influence natal philopatry in migratory passerines

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Natal philopatry (hereafter, philopatry) is breeding at or near an individual's place of origin (Weatherhead & Forbes, 1994). Human development and agriculture have created heterogeneous landscapes that often fragment and isolate habitats, forcing individuals to either return to their natal patch (be philopatric) or disperse to another (Fischer & Lindenmayer, 2007). Philopatry rates tend to be higher in more isolated patches (e.g. Hansson et al., 2003, Potti and Montalvo, 1991, Wheelwright and Mauck, 1998), even among populations of the same species (Weatherhead & Forbes, 1994). High philopatry rates can have a variety of effects on individual fitness: they can increase the risk of inbreeding depression (Keller & Waller, 2002), but philopatric individuals can also have a mating advantage or increased reproductive success over dispersers (Bensch et al., 1998, Pärt, 1991, Pärt, 1994). Consequentially, increased philopatry also has implications for population dynamics and conservation.

Unusually high incidence of philopatry has occurred in the agricultural grassland system of Vermont and New York's Champlain Valley, where we have observed high numbers of relatively philopatric (i.e. short-distance) Savannah sparrows, *Passerculus sandwichensis*, and bobolinks, *Dolichonyx oryzivorus* (Fajardo, Strong, Perlut, & Buckley, 2009). Grassland bird species breeding in agricultural landscapes provide an excellent model for the investigation of factors affecting natal philopatry and their consequences for conservation because most of their native habitat has been replaced by agricultural lands under intense management for hay and pasture (Hannah, Carr, & Lankerani, 1995). These management schemes can have strong effects on average reproductive success depending on the timing of mowing and grazing, causing near zero reproductive success on some fields (Perlut, Strong, Donovan, & Buckley, 2006). Thus, the majority of locally fledged individuals originate in relatively high-quality areas, and philopatry or dispersing to habitat similar to the natal area would be a good dispersal strategy. However, management effects on environmental cues, changes in management strategy and factors intrinsic to the individual could reduce the likelihood an individual will make a good breeding site choice. Understanding of the factors that directly influence an individual's level of philopatry could lead to effective land management strategies that reduce the likelihood of settlement in poor-quality areas and encourage settlement in high-quality areas, and these strategies would be especially useful for declining species that require conservation in landscapes dominated and fragmented by human development and agriculture.

Relatively little is known about the proximate, or immediate, factors that influence an individual's decision to breed near its place of origin, especially in migratory passerines. In this study, we attempt to

answer two questions. (1) Which intrinsic, social or environmental factors most strongly influence how close an individual will breed to its natal site? (2) Are grassland birds able to respond to these factors when making philopatry decisions, even when the factors are distributed based on the artificial boundaries created by human land management?

To investigate these questions we used two metrics: natal dispersal distance and natal field fidelity. Natal dispersal distance allows us to determine how factors may influence absolute distance regardless of field size, shape and distribution, while natal field fidelity allows us to determine whether the birds are using man-made field boundaries when evaluating the natal field as a breeding site. Given the importance of human land management on the fitness of birds in this system, a bird's ability to evaluate the habitat using the same boundaries as its human managers would be beneficial when making dispersal decisions. Based on the available literature concerning natal philopatry and dispersal of migratory passerines, and observations from our own study system, we chose to estimate the effects of seven potential proximate influences on philopatry (Clobert et al., 2009, Doligez and Pärt, 2008, Fajardo et al., 2009, Greenwood, 1980, Payne, 1991, Perkins et al., 2013). These seven influences were divided into three categories based on each influence's source: intrinsic, extrinsic social and extrinsic environmental. We predicted that two intrinsic characteristics influence philopatry: (1) sex, where males will be more philopatric than females because they are thought to benefit more from familiarity with an area (Greenwood, 1980); and (2) fledge date, where late-fledging birds will be more philopatric than early fledging birds because they have less time to disperse postfledging and evaluate potential breeding sites (Dhondt and Hublé, 1968, Nilsson, 1989, Payne, 1991). We predicted that three extrinsic social conditions influence philopatry: (1) opposite-sex relative presence, where birds with an opposite-sex relative (parent or sibling) present on the natal field the year they start breeding will be less philopatric than birds without a relative present to avoid inbreeding (Greenwood, 1980); (2) average reproductive success, where birds will be more philopatric if they observe high average reproductive success on their natal field the year prior to settlement (Calabuig et al., 2008, Pärt and Doligez, 2003); and (3) breeding density, where birds will be more philopatric if they observe high conspecific breeding density on their natal field in the year prior to settlement (Nocera, Forbes, & Giraldeau, 2006). We predicted that the extrinsic environmental factor agricultural management would influence philopatry, where birds would be more philopatric when their natal field is under a management scheme that allows for high reproductive success and creates an attractive vegetation structure during habitat evaluation (Fajardo et al., 2009). We also discuss the implications that our findings have for management and conservation of migratory passerines living in heterogeneous landscapes.

Methods

Study Area

Our research took place during 2002–2014 within the Champlain Valley of Vermont, a region containing approximately 146 000 ha of managed grassland (National Agriculture Statistics Survey, 2010). We established a study area in Shelburne, VT, U.S.A. (44°23'40.542"N, 73°15'30.7908"W), which consisted of a mosaic of grasslands, forest and human developed areas (Fig. 1). All grasslands were divided into agricultural fields and managed under one of five schemes: (1) early-hayed (EH): first hayed between 27

May and 11 June, and hayed again in early to mid-July; (2) middle-hayed (MH): hayed between 21 June and 10 July; (3) late-hayed (LH): hayed after 1 August; (4) gap-hayed (GH): first hayed before 31 May and again at least 65 days later; (5) rotationally grazed pastures (RG): fields in which cows were rotated through a matrix of paddocks with multiple week 'rests' between grazing events (for further details, see Perlut et al., 2011, Perlut et al., 2006). Our five main study fields, where bird demographic data were collected, ranged in size from 16.3 to 19 ha. Other fields within the landscape ranged from 1.9 to 40.4 ha. Grasslands were irregularly spread throughout the landscape; individual grassland fields were rarely adjacent to other agricultural fields (grassland and/or row crop) on all sides, most often adjacent to other agricultural fields on one to two sides, and sometimes completely isolated from other agricultural fields by forest or human development (Fig. 1).



Figure 1. Study area at Shelburne, VT, U.S.A. The landscape is a mix of forest, agricultural fields and human development. Grasslands and row crop are indistinguishable from aerial images, and the majority of open areas within this landscape were identified on the ground as row crop. Areas covered by diagonal lines are the five focal fields where demographic information on bobolinks and Savannah sparrows was collected. We searched for banded birds in the white-covered areas during 2005–2014, and grey-covered areas during 2014.

Study Species

Both study species are grassland-obligate, solitary nesting passerines and constitute more than 92% of the grassland-obligate breeding birds in our study system (Perlut et al., 2006, Shustack, 2004). These species differ in both migration and breeding strategies. Bobolinks are long-distance migrants, wintering

in Argentina, South America (Renfrew et al., 2013, Renfrew et al. 2015). Their breeding season in Vermont spans from late May to late July, during which a female will usually make a single nest attempt, although reneesting sometimes occurs (Perlut et al., 2006). Savannah sparrows are short-distance migrants, wintering in the southern United States and Mexico (Wheelwright & Rising, 2008). Their breeding season spans early May to mid-August, and females can make several nest attempts during a single season (Perlut et al., 2006). Individuals of both species begin breeding as 1-year-olds and attempt to breed each year (Fajardo et al., 2009, Wheelwright and Rising, 2008).

Agricultural management has strong effects on the reproductive success and apparent survival rates of these two species (Perlut et al., 2006, Perlut et al., 2008a). Average reproductive success and apparent survival are both highest on late-hayed fields and lowest on early-hayed fields, representing high- and low-quality agricultural habitat, respectively (Perlut et al., 2006). Each species responds to haying differently; Savannah sparrows stay and immediately reneest, whereas bobolinks abandon the field for about 2 weeks after the field is mowed (Perlut et al., 2006).

Fieldwork

We collected breeding and genetic data on individual bobolinks and Savannah sparrows at five study fields following Perlut et al., 2006, Perlut et al., 2008b. All adult birds were wild-caught using mist nets, and nestlings were temporarily removed from their nests by hand on day 6–7 to be banded, measured and bled on site. Adult individuals were marked by unique combinations of three colour leg bands and a single metal U.S. Geological Survey (USGS) band, while nestlings were marked with a single metal USGS band (Perlut et al., 2006). We collected a small (20–60 μ l) blood sample from the brachial vein for DNA analysis from individuals when they were initially banded and once per year if captured in subsequent years (Perlut, Freeman-Gallant, et al., 2008). We strove to limit stressful impacts of handling, banding and bleeding birds by minimizing the time and frequency we handled birds. Appropriate animal care was approved under the Institutional Animal Care and Use Committee of the University of New England (protocol number UNE010-2009), and banding was conducted under U.S. federal permit number 23540.

We searched for adults originally banded as nestlings, identifiable by their single metal band, with binoculars each year. We searched weekly on study fields in all years, and searched all fields within a 1.5 km radius of the study fields at least twice during 2005–2014 following methods described in Perlut, Strong, et al. (2008) and Fajardo et al. (2009) (Fig. 1). The estimated detection probability using these search methods is 0.69 (Perlut, Strong, et al., 2008). In 2014, we used satellite images to identify agricultural fields larger than 4 ha within a 10 km radius of the study fields to search; it was impossible to differentiate grassland from row crop from these images, so we searched all potential grassland fields once (N = 88 fields, 1110.11 ha) and all actual grassland fields at least twice following search methods described by Perlut, Strong, et al. (2008; Fig. 1). The increase in search area during 2014 did not substantially change the observed average dispersal distance because only four birds were found in the extended search radius and all were within 5 km of the study fields. We recaptured birds banded as nestlings to identify them and gave them unique colour band combinations. We also attempted to band their mates and find their nests. We recorded the GPS location of each individual at first capture and of their nest if found.

Data Analysis

We used two metrics to measure every individual's level of philopatry: whether a bird attempted to breed on its natal field (natal field philopatry) and its natal dispersal distance. Our natal dispersal distance data set considered only individuals that dispersed within 3 km, as our limited resources prevented us from searching areas greater than 3 km from our study fields in most years. Natal dispersal distance was defined as the distance between an individual's natal nest and location of first detected breeding attempt, which was either the location of the individual's first breeding nest or location of capture (distances were calculated in metres using the distance tool in ArcMap 10.0; ESRI, 2011). We considered a bird a breeder if it was associated with a nest or there was evidence that it was attempting to breed, such as territory and mate defence for males, or a brood patch and signs of egg development for females.

Forty per cent of the bobolink dispersers and 17% of the Savannah sparrow dispersers in our study were older than 1 year old at first detection (average age at first detection was 1.7 for bobolinks and 1.4 years for Savannah sparrows), so it is possible the dispersal distances recorded for these individuals did not reflect natal dispersal because they could have also undergone breeding dispersal (dispersed a second time after breeding and before detection; Fajardo et al., 2009, Wheelwright and Rising, 2008). However, we included these individuals in the data set because they were most likely representative of natal dispersal. Our measured distances were unlikely to change substantially due to breeding dispersal because over 80% of the adults in our population that underwent breeding dispersal returned to the same field, which resulted in an average breeding dispersal distance that was eight times lower than the average natal dispersal distance (Fajardo et al., 2009). Nevertheless, we included age as an explanatory factor in the bobolink dispersal distance analysis because we detected a larger proportion of bobolink dispersers after their first breeding year; we compared second-year (SY) birds to after second-year (ASY) birds to account for differences in experience that may have affected dispersal distance.

We developed a priori mixed-effect and logistic regression models to investigate how intrinsic, social extrinsic and environmental extrinsic proximate factors on the natal field influenced natal dispersal distance and natal field philopatry, respectively. We investigated the following factors: sex, fledge date (FD), average number of fledglings per female (i.e. reproductive success; RS) and number of females per hectare (i.e. breeding density; BD) on the natal field during the year before an individual settled, presence/absence of opposite-sex relatives on the natal field during the year of settlement (OSR) and management scheme of the natal field during the individual's hatch year (MT) (Clobert et al., 2009, Fajardo et al., 2009, Greenwood, 1980, Hansson et al., 2003, Nocera et al., 2006, Pärt, 1990, Pärt and Doligez, 2003, Perkins et al., 2013, Wheelwright and Mauck, 1998). All continuous explanatory variables (FD, RS and BD) were Z-standardized. We developed four sets of models, one for each species' natal dispersal distance and natal field philopatry. We separated our analyses by species and response variables to reduce the likelihood of obtaining type I errors, as the total number of relevant predictor variables increased dramatically due to the need to include interactions between species and other predictors. All data within each model set were independent because there was one data point for each individual per response variable.

The natal dispersal distance model sets for both species consisted of linear mixed-effect models that included hatch year, natal field and breeding field (BF) as random effects to account for spatial and time effects. The global model for bobolink natal dispersal distance included sex, fledge date, management, age and age*fledge date as fixed effects, while the global model for Savannah sparrows included sex, fledge date and management. When the global model was run to assess fit to the data for each species, the random effects hatch year and natal field explained zero variance, so they were dropped from all subsequent models (Bates, 2010). Social and other environmental factors on the natal field were not included in the dispersal distance sets after we determined that their heterogeneity across the landscape would make their potential effects on dispersal distance nonlinear. For example, if individuals that hatched on a field with low reproductive success used that metric as a cue to disperse from that low-quality area, their dispersal distances would be high enough to leave the natal field, but we would not expect the natal field cue to influence dispersal distance past the edge of the field. Instead, model sets for both species included the distance to the field with the highest breeding density in the individual's hatch year (DIST) to investigate the effect of social factors. The null models for both dispersal distance sets contained only the random effect BF, and the rest of the models in each set contained BF and some combination of the fixed effects. The final dispersal distance model sets contained 14 models for bobolinks and eight models for sparrows (Supplementary Tables S1 and S2).

The model sets for natal field philopatry included logistic regression models. The bobolink global model included sex, fledge date, age, reproductive success, breeding density, opposite-sex relative presence, management age*reproductive success and age*fledge date, while the Savannah sparrow global model included sex, fledge date, breeding density, opposite-sex relative presence and management. The null model contained no explanatory variables (i.e. just the y intercept) while all other models contained some combination of the y intercept and at least one of the explanatory variables included in the global model for each species. We did not include reproductive success in the Savannah sparrow set because the synchrony of breeding in this species prevents postfledging birds from easily assessing this type of public information, and while bobolinks are also synchronous breeders, enough of our observations were of after-second year birds that would have had an opportunity to evaluate public information as adults. The final natal field philopatry model sets contained 24 models for bobolinks and 20 models for Savannah sparrows (Supplementary Tables S3 and S4).

We ranked models using Akaike's information criterion corrected for small sample sizes (AICc) and calculated $\Delta AICc$ and AICc weights (ω_i) (Burnham & Anderson, 2002). Models were considered biologically significant if $\Delta AICc \leq 2$ relative to the best model. We calculated regression coefficient estimates and 95% confidence intervals for factors included in biologically significant models. If a factor was included in more than one biologically significant model, we calculated model-averaged estimates. We considered individual factor effects, as reflected in their regression coefficients for fixed effects (β) or variance coefficients for random effects (σ), biologically significant if their 95% confidence intervals did not include zero. We ran all statistical analyses in R version 3.1.3 (R Core Team, 2014). We ran mixed-effect models using the 'lme4' package (Bates, Maechler, Bolker, & Walker, 2014) and calculated AICc values using the package 'AICcmoavg' (Mazerolle, 2015).

Molecular Analyses

We analysed seven hypervariable microsatellite loci to conduct paternity analyses on a subset of 43 locally hatched Savannah sparrows: Psa12 and Psa29, *P. sandwichensis* (Freeman-Gallant, Wheelwright, Meicklejohn, States, & Sollecito, 2005); Escu6, *Emberiza schoeniclus* (Hanotte, Zanon, & Pugh, 1994); Mme1 and Mme8, *Melospiza melodia* (Jeffery, Keller, Arcese, & Bruford, 2001); and Psap61 and Psap335, *P. s. princeps* (Temple, 2000). All PCR reactions had a total volume of 15 μ l and contained 1 μ l of 50 ng/ μ l DNA, 0.5 U Taq polymerase and 1 \times PCR buffer (Invitrogen, Inc., Carlsbad, CA, U.S.A.). Locus-specific annealing temperatures and concentrations of MgCl₂, dNTPs, primers and BSA are provided in Supplementary Table S5.

We used CERVUS software to assess allele frequencies, estimate heterozygosities, calculate observed heterozygosities, estimate null allele frequencies, test for Hardy–Weinberg equilibrium and calculate exclusion probabilities for all loci (see Supplementary Table S6). Two of the loci, Mme1 and Psap61, had estimated null allele frequencies higher than 0.05, so they were removed from further paternity analysis. The probability of exclusion for the combined set of the five remaining loci was $p = 4.2 \times 10^{-4}$. We also used CERVUS to assign paternity at the 95% confidence level using the four autosomal-inherited loci Psa12, Mme8, Escu6 and Psap335 (Kalinowski, Taper, & Marshall, 2007). When CERVUS identified two equally likely fathers that matched an offspring at all loci, we used the Z-linked Psa29 to determine the identity of the father.

Results

Summary Statistics

We detected 129 locally hatched bobolinks (50 females, 79 males) and 90 locally hatched Savannah sparrows (35 females, 55 males), representing 31% and 18%, respectively, of the banded nestlings expected to survive to adulthood (percentages calculated using survival estimates from our populations, Perlut & Strong, in press; Table 1). Of these, 27 bobolinks (21%, 9 females, 18 males) and 33 Savannah sparrows (39%, 15 females, 18 males) bred on their natal field. Two long-distance dispersers were also found opportunistically, but were not included in this analysis: one female bobolink was found 8.4 km away, and one female Savannah sparrow was found 33.9 km away.

Table 1. Summary statistics for bobolink and Savannah sparrow natal dispersal distances in the Champlain Valley of Vermont, U.S.A., 2002–2014

Species	Mean (m)	SD	Median (m)	Min. (m)	Max. (m)	N
Bobolink	1251.2	839.0	1058.3	12.0	3538.2	129
Savannah sparrow	916.7	851.1	917.1	13.2	4933.4	90

Bobolink Natal Dispersal Distance

Five models had $\Delta AIC_c \leq 2$ relative to the top-ranked model (Table 2). Sex was included in the top-, second-, fifth- and sixth-ranked models (cumulative $\omega_i = 0.46$), and while males tended to disperse shorter distances than females, this effect was not biologically significant ($\beta = -185.01$, 95% CI: $-394.71, 24.88$). Age at first detected breeding was also included in the second- and fourth-ranked models (cumulative $\omega_i = 0.23$), and although SY birds tended to disperse slightly shorter distances than ASY birds, the effect was small relative to average field size and was not biologically significant ($\beta = -141.62$, 95% CI: $-350.12, 71.08$). Distance to field with highest breeding density and fledge date were in the fifth- and sixth-ranked models, respectively ($\omega_i = 0.07$ for both), but neither had an effect on dispersal distance ($\beta = 33.73$, 95% CI: $-67.78, 135.17$; $\beta = 32.92$, 95% CI: $-74.59, 137.37$, respectively). The null model, which included only the random effect BF, was the third-ranked model ($\omega_i = 0.12$). Therefore, while there was some evidence that sex, age, fledge date and breeding density influenced bobolink dispersal distance, their effects were not strong. In all six of these models, the random effect of breeding field explained about half of the variation unexplained by fixed effects (BF: $\sigma = 778.20$, 95% CI: $446.37, 1277.10$; residual: $\sigma = 562.88$, 95% CI: $495.49, 641.56$). Birds that bred on or near study fields under management schemes that allowed for relatively high reproductive success dispersed shorter distances on average than birds that bred on fields far from productive study fields.

Table 2. Candidate models with $\Delta AIC_c \leq 2$ of natal dispersal distance and natal field philopatry for boblinks and Savannah sparrows

Model set	Rank	Model description	No. of parameters	ΔAIC_c	ω_i
Natal dispersal					
Bobolink	1	Sex+BF	2	0	0.17
	2	Sex+age+BF	3	0.256	0.15
	3	BF	1	0.712	0.12
	4	Age+BF	2	1.472	0.08
	5	Sex+DIST+BF	3	1.735	0.07
	6	Sex+FD+BF	3	1.814	0.07
Savannah sparrow	1	BF	1	0	0.29
	2	DIST+BF	2	1.08	0.17
	3	Sex+BF	2	1.626	0.13
Natal field philopatry					
Bobolink	1	BD	1	0	0.27
	2	RS+BD	2	0.0374	0.26
	3	RS	1	1.0579	0.16
	4	Null model	0	1.4702	0.13

Model set	Rank	Model description	No. of parameters	ΔAIC_c	ω_i
	5	BD+OSP	2	1.9989	0.10
Savannah sparrow	1	FD+OSP+MT	3	0	0.37
	2	FD+BD+OSP+MT	4	1.558	0.17

Factors included in the natal dispersal models are: sex, age, fledge date (FD), distance to the field with the highest breeding density in the natal year (DIST) and breeding field (BF). Factors included in the natal field philopatry models are: breeding density (BD), average reproductive success (RS), opposite-sex relative presence/absence (OSP), fledge date (FD) and natal field management scheme (MT).

Bobolink Natal Field Philopatry

Four models had $\Delta AIC_c \leq 2$ relative to the top-ranked model (Table 2). Breeding density was in the top-, second- and fifth-ranked models (collective $\omega_i = 0.63$). Bobolinks were more likely to breed on their natal field as breeding density increased, but the effect was not biologically significant ($\beta = 0.41$, 95% CI: $-0.03, 0.87$). Bobolinks were also increasingly likely to breed on the natal field as reproductive success increased, and although this variable was in the second- and third-ranked models, the effect was not biologically significant (collective $\omega_i = 0.42$, $\beta = 0.40$, 95% CI: $-0.12, 1.04$). The presence/absence of an opposite-sex relative was in the fifth-ranked model, but its effect was also not biologically significant ($\omega_i = 0.10$, $\beta = 0.14$, 95% CI: $-0.76, 1.02$). The null model was ranked fourth, and its presence in the top-ranked models suggests that none of the explanatory factors had strong effects on natal field philopatry.

Savannah Sparrow Natal Dispersal Distance

Two models had $\Delta AIC_c \leq 2$ relative to the top-ranked model (Table 2). The top-ranked model ($\omega_i = 0.29$) only included the breeding field random effect, suggesting that none of the other explanatory factors explained variation in dispersal distance. The second-ranked model included distance to field with highest breeding density in natal year and breeding field ($\omega_i = 0.17$), but the slight positive effect of breeding density was not biologically significant ($\beta = 94.74$, 95% CI: $-83.66, 378.47$). Similarly, the effect of sex in the third-ranked model ($\omega_i = 0.13$) was also not biologically significant ($\beta = 94.64$, 95% CI: $-153.99, 347.66$). Most of the variation was due to BF ($\sigma = 1094.52$, 95% CI: $692.12, 1698.35$; residual: $\sigma = 521.23$, 95% CI: $445.28, 620.39$) where birds breeding on or near fields under management schemes that allowed for relatively high reproductive success dispersed shorter distances, on average, indicating that Savannah sparrow dispersal distances mostly depended on spatial effects.

Savannah Sparrow Natal Field Philopatry

Only one model had $\Delta AIC_c \leq 2$ relative to the top-ranked model (Table 2); both the best- and second-ranked models included fledge date, presence/absence of an opposite-sex relative and management scheme, and all of their effects were biologically significant (collective $\omega_i = 0.43$). Savannah sparrows were increasingly likely to breed on the natal field as fledge date increased ($\beta = 0.61$, 95% CI: $0.04, 1.23$) and were less likely to breed on the natal field if an opposite-sex relative was present the year they

began breeding ($\beta = -1.63$, 95% CI: $-2.79, -0.59$; Fig. 2). Of the three management schemes considered (early-hayed, late-hayed, gap-hayed), natal field philopatry differed between Savannah sparrows hatched on gap-hayed fields and those hatched on late-hayed fields, where birds were more likely to return to gap-hayed fields ($\beta = 1.45$, 95% CI: $0.002, 2.89$; Fig. 2). Breeding density was also included in the second-ranked model, but its effect was not biologically significant ($\beta = 0.29$, 95% CI: $-0.35, 0.96$). Therefore, fledge date, opposite-sex relative presence/absence and management scheme had the strongest effects on Savannah sparrow natal field philopatry.

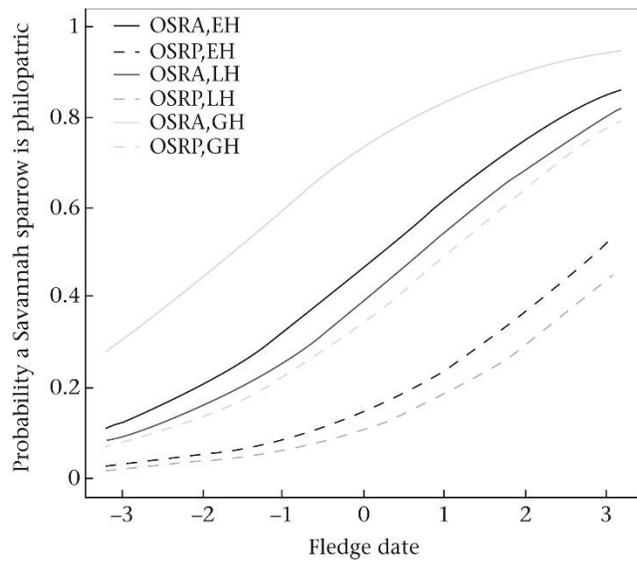


Figure 2. Probability curves for Savannah sparrow natal field philopatry explained by combinations of natal field management (late-hayed (LH), early-hayed (EH), or gap-hayed (GH)) and presence (OSRP)/absence (OSRA) of opposite-sex relatives on the natal field and Z-standardized fledge date. Fledge date ranges from 9 May to 24 August.

Discussion

In semi-contiguous habitat within large landscapes, migratory songbirds rarely return to breed near their natal site (e.g. 0% documented for Savannah sparrows by Bédard & LaPointe, 1984). However, in the Champlain Valley of Vermont, Savannah sparrow and bobolink philopatry rates are relatively high (reviewed in Weatherhead & Forbes, 1994); these rates are similar to rates observed in isolated populations of these species inhabiting natural island habitat (Wheelwright and Mauck, 1998, Wittenberger, 1978) but much higher than populations in semi-contiguous natural habitat (Bédard & LaPointe, 1984). This philopatry allowed us to investigate the proximate influences on this behaviour in detail. We found that bobolink short-distance natal dispersal and natal field philopatry were not influenced by the intrinsic characteristics and extrinsic natal conditions we measured, while a combination of intrinsic, social and environmental characteristics had the most influence on these natal

field philopatry behaviours in the Savannah sparrow. These two species differ in several behavioural aspects that may be responsible for their dissimilar responses to dispersal cues. The most conspicuous difference lies in their behavioural responses to agricultural management; when a field is mowed before the nesting cycle is complete, bobolinks abandon the field temporarily and either return to breed, breed elsewhere, or become floaters, whereas Savannah sparrows stay on their territories and immediately reneest (Perlut et al., 2006). Fajardo et al. (2009) found that Savannah sparrows were also more likely to make unfavourable decisions with regard to management scheme if they dispersed after breeding at their initial site, while bobolinks were more likely to make favourable breeding dispersal decisions. Thus, there may be more selective pressure on Savannah sparrows to make good natal dispersal decisions, and intrinsic influences would be most effective in guiding inexperienced birds to good choices. Additionally, if natal dispersal decisions are less important to bobolinks because they are forced to disperse more often by agricultural management and are better at evaluating habitat for breeding dispersal decisions, they should not be strongly influenced by intrinsic characteristics or natal field conditions. Instead, they would be more influenced by cues exhibited by potential breeding sites other than the natal field, such as conspecific reproductive success, breeding densities or habitat structure. The differences in the dispersal and philopatry of these species also highlight the fact that conservation plans for a group of species inhabiting the same habitat should not be based on study of a single representative species.

Natal field management did not influence short-distance natal dispersal of either study species, and there are a number of possible reasons: (1) birds may choose to leave fields under schemes that create poor-quality habitat, but once the bird has dispersed off the natal field, this influence would not continue to affect their breeding site choice; (2) birds may choose to breed on fields with the same scheme as the natal field (as found in bobolinks for this study system; Fajardo et al., 2009), but because management is not consistent across the landscape or over time due to weather constraints (Perlut, Strong, et al., 2008), this behaviour leads to seemingly random dispersal distances; or (3) birds do not use habitat cues associated with management during dispersal. Management does influence a social cue that other species use to inform dispersal decisions, previous reproductive success in an area (Perlut et al., 2006). Past reproductive success influences immigration and emigration rates in fragmented passerine populations, and colony choice in some nonpasserine species (e.g. Calabuig et al., 2008, Doligez et al., 2004, Parejo et al., 2007). While this cue can affect dispersal decisions, it would not consistently affect dispersal distance in heterogeneous landscapes like our study system, where areas with high average reproductive success are randomly distributed across the landscape.

For both species, we observed notable philopatry to the natal field. Similar behaviour in passerines has most often been reported from populations residing within insular, limited or fragmented habitats (e.g. Pärt, 1990, Potti and Montalvo, 1991, Wheelwright and Mauck, 1998, Wittenberger, 1978). This behaviour suggests that some of our study fields were seen as high-quality habitat compared to immediately surrounding grassland areas and, therefore, philopatry to certain fields could be considered an adaptive strategy. However, Savannah sparrows and bobolinks appeared to use different cues when evaluating the suitability of their natal field as a breeding site.

Bobolink natal field philopatry was random with regard to intrinsic and environmental variables, but there were weak trends associated with public information cues. The probability a bobolink bred on its natal field tended to increase as average reproductive success and breeding density on the natal field increased, which suggests that conspecific success and breeding activity served as attractants. These types of public information cues are used by other migratory passerines, including a different population of bobolinks (Clobert et al., 2009, Doligez et al., 2004, Nocera et al., 2006). It is possible that we did not find a stronger association between natal field philopatry and these variables because bobolinks can choose to breed on other fields with high reproductive success and breeding densities. Fajardo et al. (2009) found that natal dispersing bobolinks were more likely to breed on fields under the same management scheme as their natal field, and the majority of bobolink dispersers originate in high-quality habitat. Our results suggest that bobolinks may not be cueing into the management scheme directly but observing the high reproductive success and breeding densities associated with schemes that allow time for them to breed successfully. More study on breeding field selection is needed to confirm this hypothesis.

Savannah sparrow natal field philopatry was influenced by a combination of different characteristics. We found that dispersers avoided breeding on the natal field if an opposite-sex relative was present, possibly as a mechanism to avoid inbreeding. In an island-breeding population with limited habitat availability, Savannah sparrows avoided opposite-sex relatives, so it is reasonable to expect them to show similar avoidance behaviours in a larger landscape (Wheelwright & Mauck, 1998). While fledge date did not have an effect on dispersal distance, similar to some studies (Pärt, 1990, Wheelwright and Mauck, 1998) but in contrast to others (Dhondt and Hublé, 1968, Nilsson, 1989, Payne, 1991), fledging at a later date increased the likelihood a bird would breed on the natal field. This dissimilarity between fledge date's effect on dispersal distance versus natal field philopatry may be due to individual differences in postfledging behaviour and the amount of time the birds have to explore potential breeding habitats before migration (Morton, Wakamatsu, Pereyra, & Morton, 1991). The pattern of increasing philopatry could increase the probability of inbreeding, as annual adult survival in this population is high (Perlut, Strong, et al., 2008) and more than 90% of adults that survive to the next year return to the same field (Fajardo et al., 2009). However, avoidance of nesting near opposite-sex relatives would help to reduce the probability of inbreeding.

The only extrinsic influence on Savannah sparrow natal field philopatry was management scheme, but how it affected philopatry was unexpected. The birds' response to management would be adaptive if they had been more likely to be philopatric to late- and gap-hayed fields than early-hayed fields (Perlut et al., 2011, Perlut et al., 2006). However, the only difference we found was an increased probability of philopatry to gap-hayed compared to late-hayed fields, with the likelihood of philopatry to early-hayed fields between them. Survival is highest and recruitment is lowest on late-hayed fields, which lowers the availability of breeding sites relative to other fields and possibly reduces the probability of philopatry (Perlut, Strong, et al., 2008). Survival and recruitment have not been measured for gap-hayed fields, so it is possible that survival was lower and made it easier for more birds to be philopatric. Differences in fledge dates caused by management may also influence this dynamic: fledge dates are more synchronous and delayed on gap-hayed fields than on late-hayed fields because the first mow in May

resets the breeding schedule (Perlut et al., 2006). Delayed fledge dates increase the probability of philopatry, which could contribute to the increased likelihood of philopatry to gap-hayed fields.

Conclusions

Natal philopatry is known to be an adaptive strategy for some species (Bensch et al., 1998, Pärt, 1991, Pärt, 1994); however, it is a complicated dispersal strategy in agricultural systems because it can be a good or bad decision depending on how the fields in an individual's natal area are managed (Fajardo et al., 2009). Therefore, it is important to understand what makes some individuals more philopatric than others and whether managers can influence philopatry in areas controlled by humans, especially for declining species that require conservation plans. While agricultural management dominates other aspects of grassland bird ecology, natal field management did not directly affect short-distance natal dispersal distance in either species and only affected natal field philopatry in Savannah sparrows (Perlut et al., 2006, Perlut et al., 2008a). Therefore, it is unlikely that managers will be able to easily manipulate the natal field conditions of locally hatched birds to discourage them from breeding in low-quality natal areas or encourage more of them to breed in high-quality natal areas.

Relatively high levels of philopatry do occur in this system, however, and these rates will probably increase if high-quality grassland habitat becomes more limited (Weatherhead & Forbes, 1994). High rates of philopatry increase the risk of inbreeding depression and its detrimental effects on survival and fecundity (Keller & Waller, 2002), and some populations, like our population of bobolinks, may be particularly at risk, as there was no evidence that they avoided the natal field when an opposite-sex relative was there. Additional high-quality habitat should be created to provide individuals with more breeding site options and reduce the risk of inbreeding. Managers should also focus on keeping management consistent across years, thereby reducing misinformation in dispersal cues and supporting reproductive success.

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