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

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Knowledge of which cues attract birds back to natal areas is important for conservation because the cues could be manipulated to attract breeders to source habitat or discourage breeders from settling in sink habitat. We examined the influence of intrinsic and extrinsic variables on natal philopatry using two metrics, short-distance natal dispersal and the probability of philopatry to the natal field, in two obligate-grassland bird species breeding in an agricultural landscape: the bobolink, *Dolichonyx oryzivorus*, and the Savannah sparrow, *Passerculus sandwichensis*. During 2002–2014, we detected 90 locally hatched Savannah sparrows and 129 locally hatched bobolinks breeding as adults near their places of origin (mean ± SD dispersal distances: Savannah sparrows: 917 ± 851 m; bobolinks: 1251 ± 839 m). For both species, the location of the field on which they bred relative to fields where annual productivity was greater than replacement best explained variation in natal dispersal distance. The probability a Savannah sparrow was philopatric to its natal field increased if it fledged later in the season, while this probability decreased if there was an opposite-sex parent or sibling present on the natal field, or the field was under a late-hay management scheme. None of the variables considered explained variation in bobolink natal philopatry. Natal philopatry and short-distance natal dispersal in these species appear to be influenced by factors that are difficult to manage; however, land managers should attempt to keep management consistent across time to reduce misinformation in dispersal cues.

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, Bensch, & Hasselquist, 2003; Potti & Montalvo, 1991; Wheelwright & 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, Hasselquist, Nielsen, & Hansson, 1998; Pärt, 1991, 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

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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, Le Galliard, Cote, Meylan, & Massot, 2009; Doligez & Pärt, 2008; Fajardo et al., 2009; Greenwood, 1980; Payne, 1991; Perkins, Perlut, & Strong, 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 & 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, Ortego, Aparicio, & Cordero, 2008; Pärt & 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, Strong, & Alexander, 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.