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Original Article

Management Schemes, not Philopatry or Breeding Experience, Affect Nest Success of Songbirds in Vermont Hayfields

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ABSTRACT Songbirds can benefit from natal philopatry through prior knowledge about site-specific resources and local adaptation to environmental conditions. Likewise, breeding experience may also play a role in reproductive success. However, for birds that breed in managed habitats, management activities may overwhelm any potential benefits of philopatry or breeding experience. We examined the effect of site fidelity on reproductive success in 1,823 bobolink and Savannah sparrow nests in agricultural grasslands in Vermont, USA. From 2003–2019 we monitored the nests of 51 female Savannah sparrows and 72 female bobolinks that returned to breed on or near fields in which they hatched between 2002 and 2018). Using program MARK, we found that daily nest survival (DNS) differed between species and grassland treatment types and was not affected by philopatry. Bobolinks had greater DNS than Savannah sparrows, and DNS was generally greater on late-hayed fields than either early-hayed fields or rotationally-grazed pastures. Our results show that despite the potential for increased fitness through site fidelity or breeding experience, agricultural management has an equal or greater influence on female reproductive success. © 2021 The Wildlife Society.

KEY WORDS agricultural management, bobolink, grassland songbird, haying, natal philopatry, reproductive success, Savannah sparrow.

Natal philopatry occurs when an individual returns to breed at or near the site it was born, and together with natal dispersal, has a strong influence on gene flow and population dynamics (Balkiz et al. 2010, Salles et al. 2016, Phillips et al. 2017). Natal philopatry may be used as a settling rule when it is difficult to gauge habitat quality and may give novice breeders an advantage relative to settling at random (Schjorring 2001). Human activities can influence dispersal patterns (Fajardo et al. 2009), therefore it is critical to understand the relationship between natal dispersal and management and to find appropriate conservation and management strategies to protect populations that use human-impacted habitats.

There are 3 primary benefits associated with natal philopatry that may work together to increase reproductive success. First, breeding site familiarity resulting from natal philopatry may be the most important factor in determining nest success (Sedgwick 2004, Fowler 2005, Saunders et al. 2012). Previous knowledge about the nesting site may

confer an advantage in reproductive success (Ruusila et al. 2001, Balkiz et al. 2010). At the local scale, competition for high-quality nest sites between first-time and experienced breeders may force the former to less desirable sites; however, younger birds may be able to gain competitive ability with increased prior knowledge about their natal site (Schjorring 2001). Additionally, experienced females are likely to use flexible reproductive strategies based on information from previous breeding attempts, such as utilizing extra-pair fertilizations or divorce, whereas first-time breeders must use information gained before the first year of breeding (Baran and Adkins-Regan 2014). Second, individuals returning to their natal site may have local morphological or behavioral adaptations that confer fitness benefits (Balkiz et al. 2010, Phillips et al. 2017). Local adaptations are often facilitated through female-biased philopatry (Portnoy et al. 2015, Phillips et al. 2017), although they may be offset by gene flow associated with male dispersal from natal sites. Nonetheless, it is possible for local adaptations to occur if strong selection forces are present (Slatkin 1987, Portnoy et al. 2015, Salles et al. 2016). Deleterious alleles may be selected against, allowing local adaptations to strengthen (Raboam et al. 1998, Sale et al. 2009). The third benefit to natal philopatry is that

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individuals returning to their natal site may be more likely to mate with genetically similar birds, therefore strengthening co-adapted gene complexes and avoiding negative consequences associated with outbreeding (Raboam et al. 1998, Balkiz et al. 2010). Although inbreeding is generally considered deleterious, there is evidence that suggests inbreeding may not be purposefully avoided (Sale et al. 2009). Dispersal and natal philopatry are therefore key tools for optimizing viability and diversity in populations (Olano-Marin et al. 2011, Phillips et al. 2017).

Although natal philopatry may offer fitness benefits across many taxa, it is uncommon for migratory bird species (Weatherhead and Boak 1986, Weatherhead and Forbes 1994, Hansson et al. 2002). However, we identified a population of 2 migratory grassland songbird species that show high levels of natal philopatry and breed within a fragmented agricultural landscape, allowing us to test the role natal philopatry plays in reproductive success within a managed landscape. Reproductive success of the 2 species within our study system is impacted negatively by traditional agricultural practices, particularly intensive haying and grazing schedules (Perlut et al. 2006). Although reproductive success differs among fields due to the variation in the timing of hay harvest, successful nesting is possible within some management schedules (Perlut et al. 2008*b*, 2011), giving us the opportunity to examine how field management regime, breeding experience, and natal philopatry interact.

Bobolinks (*Dolichonyx oryzivorus*) and Savannah sparrows (*Passerculus sandwichensis*) are grassland-obligate migratory songbirds that nest in hayfields and pastures throughout the northeastern United States. In the Champlain Valley of Vermont, both species and sexes exhibit high levels of natal philopatry, typically returning to breed <3000 m from natal nest location (Fajardo et al. 2009, Cava et al. 2016). Savannah sparrows are short-distance migrants that breed between early-May and mid-August (Wheelwright et al. 1992), whereas bobolinks are long-distance migrants that breed between mid-May and mid-July (Renfrew et al. 2015). Previous work has identified multiple extrinsic and intrinsic factors that influence settlement decisions related to natal philopatry (Cava et al. 2016), but the outcome of settlement decisions on reproductive success is unknown.

To accurately determine factors influencing reproductive success in terms of natal philopatry, we evaluated daily nest survival (DNS) of bobolinks and Savannah sparrows. We focused only on females, as male reproductive output is impossible to assess without molecular paternity assessment of all offspring in each field in each year (Perlut et al. 2008*a*). Our objective was to identify if natal philopatry explained variation in DNS under variable hayfield management regimes for 2 species of migratory grassland songbirds breeding in agricultural fields with diverse haying and grazing schemes.

STUDY AREA

Our study took place between 2002 and 2019 in the Champlain Valley of Vermont (Fig. 1). The breeding

landscape consisted of a mosaic of agricultural fields with varying management schedules throughout the breeding season. We collected 86% of our data from 6 primary hayfields that ranged in size from 16.3 ha to 19 ha, whereas 14% of our data was collected from 11 secondary hayfields ranging in size from 1.9 ha to 40.4 ha.

Our study fields were in 5 treatment types: traditional early-hayed fields (early-hayed) were cut between 16 May and 11 June and generally again 35 to 52 days later; grassland bird incentive fields (early-delay) were cut between 16 May and 29 May and had a 65-day window between the first and second cuts (20 July to 2 Aug); middle-hayed fields (middle-hayed) were hayed between 21 June and 11 July; late-hayed fields (late-hayed) were cut after 15 July, typically after most birds have ended their reproductive season; and rotationally-grazed pastures (grazed) supported cattle for various lengths of time during the growing season (Perlut et al. 2006, Perlut et al. 2011).

METHODS

Field Methods

Beginning mid-May, we used mist-nets to capture and band breeding adults on all 6 primary study fields. We spent 1–2 full days mist-netting (30–35, 12-m mist nets per day) from 0400 to 1300 at each site to catch as many adults as possible. Adults were banded with a unique identification of 3 colored bands and one US Geological Survey (USGS) metal band. We identified each bird's sex by plumage (bobolink) or presence of a brood patch or cloacal protuberance (Savannah sparrow). We searched each study field for nests every 1 to 2 days throughout the breeding season, either through behavioral observations or by opportunistically flushing incubating females off nests (Perlut et al. 2006). We identified the adults associated with each nest by re-sighting color band combinations or by catching them near the nest; if they were not banded, we banded them. We monitored nests at least every 2 days until fledging or nest failure. We banded nestlings at day 5 or 6 with one metal USGS band on the right leg.

We searched our study fields weekly for adults that had been banded as a nestling (identified by the one metal band on the right leg). We recaptured birds that were banded as nestlings to identify them and give them a unique color band combination; we then located and monitored their nests following the methods described above. We also searched all fields within 1.5 km (2003–2005), 3 km (2006–2012), 10 km (2013–2017), or 20 km (2018–2019) of our study fields at least twice each year (Fajardo et al. 2009, Cava et al. 2016) for both birds originally banded as nestlings and color banded birds. Our work was approved by the University of New England's IACUC (Protocol Number: 040618-001) and U.S. Geological Survey Master Bander permit #23540.

Statistical Analysis

We classified females in 1 of 3 categories: philopatric, novice, or experienced. We considered females to be philopatric when they were banded as a nestling with a single



Figure 1. Study area at Shelburne, VT, USA, during 2002–2019. The five focal fields where we collected demographic information on Savannah sparrows (A) and bobolinks (B) are noted in black. We searched for banded philopatric birds in the dark gray patches. The light gray patches indicate non-grass agricultural fields or forests.

metal band and had returned to or near their natal field to breed, regardless of age and breeding experience. A novice female was a bird that was color banded on our study fields as an adult and assumed to not have been hatched on one of our 6 primary fields (neither species can be aged by plumage [Pyle 1997]). An experienced female was a bird that was color banded in a previous year as a breeding adult and returned in one or more consecutive years to breed on any study field but was not hatched on that field. Experienced females are similar to novice females in that they were caught as a non-banded adult, but differ from novice females because we banded them as adults in a previous year. We excluded first year nests of experienced females from our analyses. Since we mist-netted at each field at the

beginning of the season, as well as throughout the season, and maintained consistent resight logs on each field, we assumed that >95% of the birds on our study sites were banded.

Our analysis included three assumptions. First, we assumed that most adult birds on our study fields were captured and banded, although it is likely that some (<5%) birds went undetected for the season. Second, we assumed that we found >95% of the successful nests on our study sites and banded their respective nestlings. Third, we assumed that any non-banded adult on our study sites were novice breeders. It is possible that a small number of the non-banded adults could have been experienced breeders dispersing into our study sites, but the likelihood is low due

to high rates of breeding site fidelity of adults in this area (Fajardo et al. 2009), as well as other areas (Wittenberger 1978, Paradis et al. 1998, Scheiman et al. 2007).

We ran daily nest survival models in program MARK (White and Burnham 1999, Dinsmore and Dinsmore 2007). We aimed to explain variation in DNS through additive and interactive models with the following factors: species, treatment (early-hayed, early-delay, middle-hayed, grazed, late-hayed), and status (philopatric, novice, experienced). Previous research on our study population has shown that the 2 species respond similarly to treatment (Perlut et al. 2006), but the species-specific effects of philopatry on daily nest success are unknown. We took a cautionary approach to our assumptions by excluding nest records for experienced and novice females for 2002–2005, as we could not identify the ages or hatch location of these birds. Models were ranked using the Akaike's Information Criterion adjusted for small sample sizes (AIC_c) and the Akaike weight (w_i). We considered strongly supported models to have a ΔAIC_c of <2 and moderately supported models to have a ΔAIC_c between 2 and 4 (Anderson 2008). We interpreted biological significance within the top ranked models ($\Delta AIC_c \sim 2$) by examining beta values and their associated 95% confidence intervals. We considered factors for which the 95% confidence interval did not cross zero as biologically significant. Where appropriate we also included nest success values (daily nest survival^{nest cycle length}), where the mean nest cycle length was 24 and 25 days for Savannah sparrows and bobolinks, respectively.

RESULTS

We monitored a total of 1,823 nests (842 bobolink, 981 Savannah sparrow). Of the bobolink nests, 70, 558, and 214 were associated with philopatric, novice, and experienced females, respectively. Of the Savannah sparrow nests, 57, 573, and 351 were associated with philopatric, novice, and experienced females, respectively. We found 195 nests on early-hayed fields, 642 nests on early-delayed fields, 179 nests on middle-hayed fields, 153 nests on pastures, and 652 nests on late-hayed fields.

The top-ranking DNS model, treatment + species was much more strongly supported than the second and third ranked models (Table 1). The difference in DNS between species was biologically significant ($\beta = 0.21$, 95% CI = 0.06–0.36; Table 2), where DNS was greater in bobolinks than in Savannah sparrows (Table 1). Likewise, the differences between treatments were biologically significant, comparing late-hayed fields to early-hayed ($\beta = -0.61$, 95% CI = -0.84–-0.37), early-delay ($\beta = -0.25$, 95% CI = -0.42–-0.07), and grazed fields ($\beta = -0.74$, 95% CI = -0.99–-0.50), but not to middle-hayed fields ($\beta = -0.19$, 95% CI = 0.45–0.07). Here, DNS was greater on late-hayed fields as compared to early-hayed, early-delay, or grazed fields, but not middle-hayed fields (Table 2). Notably, DNS was greater on early-delay fields than early-hayed fields. All models including status were >4 AIC from the top-ranked model. For both species, differences in DNS

and nest success were indistinguishable among novice, philopatric, and experienced individuals across all management treatments (Table 2).

DISCUSSION

Our results align with previous studies indicating that grassland management schemes broadly explain variation in DNS for bobolinks and Savannah sparrows (Perlut et al. 2006; Perlut et al. 2008b, 2011). Late-hayed fields had the greatest DNS in comparison to early-hayed, early-delay, and pastures, but not middle-hayed fields; these results are in accordance with previous work conducted on our study population, although that study did not include early-delay treatment (Perlut et al. 2006). We identified no reproductive benefit associated with natal philopatry in female Savannah sparrows and bobolinks in our population, compared to experienced and novice breeders. Although high rates of natal philopatry are uncommon in migratory species (Weatherhead and Boak 1986, Weatherhead and Forbes 1994, Hansson et al. 2002), there have been several documented cases in isolated populations (Wittenberger 1978, Wheelwright and Mauck 1998, Martin et al. 2008, Forschler et al. 2010). Rates of natal philopatry similar to our study population are known for Savannah sparrows breeding on an island habitat (Wheelwright and Mauck 1998), but not in other mainland populations (Wheelwright and Rising 2008). Although comparable natal philopatry has not been documented in other populations of bobolinks (Renfrew et al. 2015), there has been some evidence of an isolated population experiencing a lower degree of natal philopatry (Wittenberger 1978). Natal philopatry in isolated populations likely occurs due to clustering of food and mates resulting from highly isolated or fragmented habitat (Greenwood and Harvey 1982, Weatherhead and Forbes 1994). Even though the Champlain Valley offers 130,000 ha of potential grassland habitat including over 32,500 grassland patches, the area is isolated from other suitable breeding habitats (Sutti et al. 2017).

Table 1. Daily nest survival models for bobolinks and Savannah sparrows breeding in hayfields and pastures in the Champlain Valley of Vermont, USA, 2002–2019. Models were ranked using the Akaike's Information Criterion adjusted for small sample sizes (AIC_c), the number of parameters (k) and the Akaike weight (w_i). We considered strongly supported models to have a ΔAIC_c of <2 . We explained variation in daily nest survival through additive and interactive models with the following factors: species (bobolink, Savannah sparrows), treatment (early-hayed, early-delay, middle-hayed, grazed, late-hayed) and status (philopatric, novice, experienced).

Model	AIC_c	k	ΔAIC_c	w_i
treatment + species	6561.8	6	0.00	0.88
status + treatment	6567.6	7	5.78	0.05
treatment	6567.7	5	5.90	0.05
treatment * species	6569.0	10	7.22	0.02
status * treatment	6579.5	15	17.66	0.00
status * species	6599.6	6	37.78	0.00
species	6599.6	2	37.81	0.00
status + species	6599.6	4	37.84	0.00
status	6620.3	3	58.54	0.00
null	6620.8	1	58.99	0.00

Table 2. Daily nest survival (DNS) and nest success (NS) values, including their respective lower and upper confidence intervals, for philopatric, experienced, and novice bobolinks and Savannah sparrows breeding in hayfields and pastures in the Champlain Valley of Vermont, USA, 2002–2019. Nest success was calculated ($DNS^{\text{nest cycle length}}$) with a 24 and 25 day nest cycle for Savannah sparrows and bobolinks, respectively.

Species	Treatment	Status	Daily nest survival			Nest success		
			DNS	LCI	UCI	NS	LCI	UCI
Savannah sparrow	Late-hayed	Philopatric	0.96	0.954	0.966	0.377	0.323	0.436
		Novice	0.96	0.953	0.965	0.373	0.315	0.425
		Experienced	0.96	0.953	0.965	0.372	0.315	0.425
	Early-hayed	Philopatric	0.929	0.899	0.95	0.169	0.078	0.292
		Novice	0.928	0.897	0.95	0.166	0.074	0.292
		Experienced	0.928	0.897	0.95	0.165	0.074	0.292
	Early-delay	Philopatric	0.949	0.931	0.963	0.287	0.180	0.405
		Novice	0.949	0.93	0.963	0.283	0.175	0.405
		Experienced	0.949	0.93	0.963	0.283	0.175	0.405
	Middle-hayed	Philopatric	0.952	0.93	0.968	0.311	0.175	0.458
		Novice	0.952	0.929	0.968	0.307	0.171	0.458
		Experienced	0.952	0.929	0.968	0.306	0.171	0.458
	Grazed	Philopatric	0.919	0.885	0.944	0.133	0.053	0.251
		Novice	0.918	0.883	0.944	0.13	0.050	0.251
		Experienced	0.918	0.883	0.944	0.13	0.050	0.251
bobolink	Late-hayed	Philopatric	0.967	0.957	0.975	0.432	0.333	0.531
		Novice	0.967	0.956	0.975	0.427	0.325	0.531
		Experienced	0.967	0.956	0.975	0.427	0.325	0.531
	Early-hayed	Philopatric	0.94	0.904	0.963	0.216	0.080	0.390
		Novice	0.94	0.902	0.963	0.211	0.076	0.390
		Experienced	0.94	0.902	0.963	0.21	0.076	0.390
	Early-delay	Philopatric	0.958	0.935	0.973	0.342	0.186	0.504
		Novice	0.957	0.934	0.973	0.337	0.181	0.504
		Experienced	0.957	0.933	0.973	0.336	0.177	0.504
	Middle-hayed	Philopatric	0.961	0.934	0.977	0.366	0.181	0.559
		Novice	0.96	0.933	0.977	0.361	0.177	0.559
		Experienced	0.96	0.933	0.977	0.361	0.177	0.559
	Grazed	Philopatric	0.933	0.891	0.959	0.175	0.056	0.351
		Novice	0.932	0.889	0.959	0.171	0.053	0.351
		Experienced	0.932	0.889	0.959	0.17	0.053	0.351

If natal philopatry is a consequence of the isolated nature of habitat in the Champlain Valley, the benefits of prior familiarity with breeding sites may be inconsequential. This is especially true in our study system where weather patterns and changes in management goals of landowners can have important indirect effects on reproductive success through annual variation in management strategies. Although we expected natal philopatry to result in increased reproductive success, we also expected experienced breeders to show greater reproductive success relative to individuals unfamiliar with the study area (novice breeders). That all 3 breeding categories showed nearly identical within-treatment reproductive success is a clear indication that management treatment swamps the potential benefits of site fidelity. In particular, the lack of any effect of philopatry in late-hayed treatments, where management effects are eliminated, suggests that any benefits of prior experience are not manifested in reproductive outcomes.

Perlut et al. (2006) reported that Savannah sparrow nest success was 9%, 28%, 43%, and 48% on early-hayed, grazed, middle-hayed, and late-hayed fields, respectively, whereas Bobolink nest success was 5%, 21%, 32%, and 46%, respectively. Notably, early-delayed fields had greater DNS compared to early-hayed fields, increasing nest success from 16% to 28% for Savannah sparrows and from 21% to 34% for bobolinks, further indicating that this management

scheme resulted in increased productivity (Perlut et al. 2011). It is possible that DNS was affected by different nesting strategies, including variable timing of re-nesting post-hay harvest, leading to bobolinks having a higher DNS than Savannah sparrows. It is also possible that the consequences, although minimal, of edge avoidance behaviors impact DNS. Savannah sparrows are negatively impacted by nesting close to edges in agricultural habitats, whereas bobolinks are seemingly unaffected (Perkins et al. 2013).

Other factors not addressed in our study may also affect DNS. Age is known to be positively associated with reproductive success, as breeding experience plays a more important role in reproductive success than breeding effort (Hoover 2003, Mauck et al. 2012, Saunders et al. 2012). Earlier arrival dates of older and more experienced females can have an indirect effect on reproductive success due to clutches being laid earlier (Saunders et al. 2012). However, in our study system, early arrival and early onset to reproduction is an insufficient strategy given that haying can start as early as 16 May. Additionally, the rate of natal philopatry increases in Savannah sparrows with later fledge date (Cava et al. 2016). Therefore, females who fledged later in the season might not have been able to gain valuable information about the natal field because they were smaller in size and needed to spend more time on self-maintenance before fall migration (Green and Cockburn 2001,

Cava et al. 2016, Perlut and Strong 2016). Although our models did not include fledge date, it is likely that the birds that fledged later in the season did not have the competitive edge compared to counterparts that fledged earlier in the breeding season, causing decreased ability to successfully compete for suitable nesting sites and food resources (Greenwood and Harvey 1982, Nilsson 1989, Payne 1991, Ost et al. 2011). Further work should explore fledge date and other conditions of the natal environment in explaining variation in DNS within our population of philopatric females.

Our results demonstrated that agricultural management regime has a greater effect than natal philopatry on DNS. Our results also suggested that agricultural management regime has the greatest impact on DNS, rather than genetic or learned behaviors. Future research should examine potential reproductive benefits for males and the role of adult survival in natal philopatry. More importantly, future work should continue to explore the effects of habitat management on different life-cycle components, including dispersal and reproduction.

MANAGEMENT IMPLICATIONS

Our results highlighted the importance of creating landscape-scale management plans that balance agricultural production and wildlife needs. Our results also suggested that even though female bobolinks and Savannah sparrows showed natal philopatry, any benefits that might be associated with natal philopatry could not overcome the effect of agricultural management regime. Nonetheless, our results further illustrate how dynamic agricultural management plans—including intensively harvested fields—can be managed with schemes that enable reproductive success in birds. Moreover, in this case, nest success increased by encouraging hay farmers to take their first harvest as early as possible in May and then delay their second harvest for 65 days (Perlut et al. 2011). We encourage practitioners to be creative in designing agricultural management plans appropriate for the natural history of species of concern within the region.

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