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RELATIONSHIPS BETWEEN INVASIVE PLANT DENSITIES AND BREEDING BOBOLINK ABUNDANCE AND POST-FLEDGING BOBOLINK SURVIVAL IS POSITIVELY CORRELATED WITH MASS AND FLEDGE DATE

A Thesis Presented

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Kevin Tolan

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ABSTRACT

Grasslands are among the most heavily degraded biomes, and the ground-nesting birds that depend on them for breeding are the most rapidly declining guild of bird species in North America. In Vermont, forest clearing during the 19th century and expansion of modern dairy agriculture have created a mosaic of hayfields that now support a suite of these imperiled species. Although avoiding management during the breeding season has been shown to greatly increase the reproductive productivity of ground-nesting birds, doing so also permits forbs and invasive species to rapidly inundate fields such that they no longer provide suitable nesting habitat for grassland birds. I surveyed adult Bobolinks (*Dolichonyx oryzivorus*) and vegetation within 13 plots in Vermont hayfields to assess how invasive plants impact the breeding abundance of Bobolink at the early stages of territory establishment, and later during peak nesting season. Reed canary grass (*Phalaris arundinacea*), which rapidly forms tall monocultures in wet portions of fields, but is not favored for nesting, was statistically, positively correlated with male Bobolink abundance during territory establishment, however its biological significance is uncertain.

Additionally, 46 Bobolink were tagged with VHF transmitters as nestlings and subsequently radio-tracked during the post-fledging period – the period of highest mortality in many songbird species. I tracked their daily post-fledging movements, habitat use, and survivorship in 2023 and 2024. Tracked birds remained on study fields for an average of 46.2 ± 8.5 [SD] days, using areas that were disproportionately open and far from field edges. Daily survivorship was positively correlated with mass and fledge date, and the cumulative 21-day probability of survival was ~50% for a bird of average mass and fledge date. These findings highlight the importance of incorporating post-fledging ecology into grassland habitat management as part of long-term land management.

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> "Biological diversity is messy. It walks, it crawls, it swims, it swoops, it buzzes. But extinction is silent, and it has no voice other than our own."
>
> – Paul Hawken

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ABSTRACT

Grasslands are among the most heavily degraded biomes, and the ground-nesting birds that depend on them for breeding are the most rapidly declining guild of bird species in North America. In Vermont, forest clearing during the 19th century and expansion of modern dairy agriculture have created a mosaic of hayfields that now support a suite of these imperiled species. Although avoiding management during the breeding season has been shown to greatly increase the reproductive productivity of ground-nesting birds, doing so also permits forbs and invasive species to rapidly inundate fields such that they no longer provide suitable nesting habitat for grassland birds. I surveyed adult Bobolinks (*Dolichonyx oryzivorus*) and vegetation within 13 plots in Vermont hayfields to assess how invasive plants impact the breeding abundance of Bobolink at the early stages of territory establishment, and later during peak nesting season. Reed canary grass (*Phalaris arundinacea*), which rapidly forms tall monocultures in wet portions of fields, but is not favored for nesting, was statistically, positively correlated with male Bobolink abundance during territory establishment, however its biological significance is uncertain.

Introduction

Grasslands are among the most expansive biomes on the planet, comprising roughly 40% of non-polar land cover (Suttie et al. 2005). When left undisturbed, grassland vegetation, dominated by grasses, sedges, and rushes, transition to forbs and eventually woody vegetation, requiring fires or grazing by large herding herbivores to sustain graminoid cover (Suttie et al. 2005, Neary and Leonard 2020). The vegetative composition and disturbance regimes of grasslands are heavily influenced by precipitation, with wetter regions having less frequent fires and, consequently, denser vegetation than more arid environments (Sample and Mossman 1997). In the western hemisphere, the persistence of temperate grasslands like North America’s Great Plains and South America’s Pampas are partially attributable to arid conditions resulting from the rain shadow of large mountain ranges, thereby increasing fire frequency and limiting the growth of forbs (Paruelo and Jobbágy 2007, Nielsen 2018).

Globally, grasslands are among the most heavily degraded terrestrial communities. Half of the planet's grasslands have been lost since 1700 (Boakes et al. 2009), with North America's tallgrass prairies showing a 95% decrease in areal extent (Comer et al. 2018). These losses have been driven by direct anthropogenic degradations such conversion to row crops and overgrazing (Jingsheng et al. 2013), agricultural intensification (Bernath-Plaisted et al. 2023), and development-driven fragmentation (Li et al. 2012). Similarly to grassland ecosystems, birds that nest on the ground in these habitats (hereafter "grassland birds") are also highly vulnerable to anthropogenic impacts as they build nests on the ground, making them highly susceptible to management activities. For example, breeding sites mowed during the height of nesting season caused near complete failure of nests in that field (Bollinger et al. 1990, Perlut et al. 2006). As a result of intensified land management and habitat loss, grassland birds are the most rapidly declining guild of birds in North America (McCracken 2005, Hill et al. 2014, Rosenberg et al. 2019, North American Bird Conservation Initiative 2025).

The habitat preferences of grassland birds are more aligned with the physical growth form of vegetation (hereafter "structure") than with species composition (Sample and Mossman 1997). Variation in growth form across grassland vegetation provides different attributes. The tillering growth form of graminoids creates a vegetation structure that assists in the concealment of nests from ground predators (Glass and Eichholz 2023), whereas some large forbs provide an overstory above the graminoid layer that provides shade and reduced visibility from above (Martin 1971); this may be particularly important during late-May nest establishment phase, which occurs prior to grasses fully growing in while some forbs have grown to provide a protective overstory by that time (Martin 1971). The vast majority of vegetation found in Northeast grasslands, including many of our most common hay grasses, such as timothy (*Phleum pratense*), orchard (*Dactylis glomerata*), and sweet vernal (*Anthoxanthum odoratum*) are native to the Palearctic and were brought to North America by European settlers to seed pastures. Though not native, these grasses form a similar vegetative structure to native grass species such as big bluestem (*Andropogon gerardii*) and switchgrass (*Panicum virgatum*), thus providing suitable habitat for grassland birds and facilitating their eastward range expansion between the 17th and 19th centuries (Vickery and Dunwiddie 1997).

Delaying a first hay harvest until at least 15 July (hereafter "once-cut") has been frequently employed to manage hayfields in a manner that provides birds time to successfully fledge young while also maintaining open grassland habitat (Perlut et al. 2006). However, this management regime also provides time for undesirable plants to successfully reproduce, forming dense monocultures and outcompeting the forage grasses that provide the structure necessary for grassland bird nesting. In the absence of disturbance, the rapid introduction of forbs can quickly dominate and alter the vegetation structure of grasslands. Non-native forbs often rapidly colonize grasslands leading to substantial changes in habitat structure (Scharfy et al. 2011) resulting in a wide range of negative effects in grasslands (Nelson et al., 2017), though native forbs also change the vegetative structure of grasslands when left to undergo succession. Invasive plants, non-native species that spread rapidly and outcompete native species (International Union for Conservation of Nature 2000, Richardson et al. 2000), tend to flower before native species which allows for earlier reproduction (Dickson et al. 2012), and can also alter soil conditions to facilitate better growing conditions for themselves to the detriment of other species (Jordan et al. 2008). Edges created through habitat fragmentation by roads (Gieselman et al. 2013) and the use of heavy machinery, such as that used for farming activities, can facilitate the transfer of non-native or invasive plants over long distances (Fleming, 2005). As the number of dairy farms has declined and been subject to consolidation (Claro et al. 2021), the practice of one farmer haying numerous properties has become more widespread, which may have introduced invasive plants rapidly across the agricultural landscape by facilitating dispersal of seeds or other parts. In the past decade, invasive forbs have become an increasingly serious concern for long-term grassland bird conservation in the Northeast. This threat is relatively new to northeastern grassland birds, going unlisted as a barrier to population recovery in the 2014 Vermont Grassland Bird Management and Recovery Plan (LaBarr et al. 2014).

Unlike non-native forage grasses, other non-native plants like forbs and reed canary grass (*Phalaris arundinacea*) are highly invasive and can rapidly homogenize the vegetation structure. The rapid spread of invasive plants has also been shown to be negatively correlated with the diversity of plants, arthropods, and birds (Scheiman et al. 2003, Moroń et al. 2009, Skórka et al. 2010). In addition to reducing habitat quality, grasslands with heterogenous vegetative structures provide habitat for a higher diversity of grassland birds (Henderson 2025). In Poland, breeding bird diversity and the number of breeding pairs was greater in grasslands without non-native goldenrod than when it was present (Skórka et al. 2010).

Bobolinks are a relatively common breeding grassland bird in the Northeast that are frequently used as a flagship species for grassland bird conservation due to their abundance and moderate area sensitivity (Vickery et al. 1994). They exhibit a high level of sexual division of labor, with females building nests with no male assistance, and males exhibiting ritualized displays and strong territoriality (Renfrew et al. 2020). The greatest threats to Bobolink breeding habitat is the conversion of hayfield habitat to row crops or developments, as well as intensified grazing, mowing, and extreme weather events (Renfrew et al. 2019). Bobolinks rarely renest when nest failure occurs after 25 June (N. Perlut unpub. data), limiting their reproductive output if nests are destroyed by agricultural activity. Climate change is expected to further complicate the phenological mismatch between the breeding timeline of Bobolinks and agricultural land as field management is occurring earlier now than in previous decades (McGowan et al. 2021). The velocity of climate change in the United States is greatest in the central plains due to the limited topographical complexity and predicted shifts in water and temperature regimes (Dobrowski et al. 2013), and the climatic suitability of some grassland bird ranges are expected to undergo northward shifts, driven largely by changes in moisture (Nixon et al. 2016). As a result of these shifts, conservation opportunities for grassland species are expected to increase in New England, as well as the Allegheny Plateau of New York and

Pennsylvania, where grasslands are slated to become important as climate refugia (Renfrew et al. 2019).

Quantifying the impact of invasive plants will allow for the development of management regimes that integrate invasive plant control into breeding-season nesting habitat conservation. While past studies have provided preliminary evidence that invasive plants can impact birds, little is known about the relationship between the abundance of grassland birds and the density of invasive plants. While there is likely a threshold under which invasive plant species do not have a measurable impact on bird densities, as the density of invasive species increases the impacts may compound. The objective of this project was to determine if Bobolink breeding density changed across a gradient of invasive plant densities, and across the breeding season as vegetation growth progressed. This knowledge is key to understanding the tradeoff between implementing management strategies that avoid direct nest mortality and those aimed at reducing invasive plant density through intensive management.

Methods

Fieldwork

Study sites

Surveys were conducted across five hayfields in Vermont: three in Chittenden County (15, 16, and 16 ha) and two in the Missisquoi National Wildlife Refuge in Franklin County (20 and 44 ha). All study fields had been managed under a once-cut, delayed mowing management regime, and were not cut prior to 1 August for at least the prior five breeding seasons.

Study design

Between May and July of 2024, thirteen one-hectare survey plots were established >50 m from edges of grasslands, of at least 80º openness, in Shelburne, Charlotte, Ferrisburgh, and Swanton, Vermont (Figure 1). Due to the fragmented nature of the landscape, plots were placed in field centers rather than randomly distributed to ensure openness and distance to edge were relatively constant between plots. With one exception, when multiple plots were located in the same field, they were separated by at least 75 m to reduce the chances that individual birds are counted in multiple plots; in one field, plots were separated by only 50 m due to extensive flooding which limited plot arrangement options. No birds were observed moving between plots during surveys.

Two area surveys consisting of ~5 transects separated by ~20 m were conducted to quantify bird abundance in each plot. Each survey occurred between 19 May to 5 June 2024 between sunrise and 09:00 when there was no precipitation and wind was light and unlikely to hinder observations. A handheld GPS unit was used to delineate plot boundaries; given the open nature of grasslands, signal strength was consistently high and spatial accuracy was ~5 m. One or two additional area surveys were conducted between 26 June and 3 July to determine post-settlement plot abundance. Repeated surveys at each plot aimed to account for random variability during surveys.

To quantify the vegetative composition of each plot, point samples were taken along ten 100-m transects beginning 1 July, with vegetation sampled at 2 m intervals (totaling 500 points per plot). At each point, the plant species directly rooted at each sample point (hereafter "underlayer") and the dominant vegetation within a 15 cm radius of that point (hereafter "cover"); the two measurements at each point represent two distinct layers of vegetation. Due to their readily identifiable growth forms, reed canary grass, smooth bedstraw, and spotted knapweed were individually assessed during vegetation surveys; all other vegetation was classified into multiple species groups, including non-reed canary graminoid (hereafter "forage grasses"), forb (native), legume (non-native), forb (non-native, non-legume), thatch, or soil/moss. The vegetative species composition during these surveys were considered a proxy for vegetation present during the post-settlement period. The percentage of points of each vegetation classification were used as vegetative covariates.

Analysis

Invasive vegetation species captured within our study points (reed canary grass, spotted knapweed, smooth bedstraw) were pooled into a single "invasive" category. Along with thatch, which is necessary for nest construction, the pooled invasive species was compared to bird abundance at both initial settlement and post-settlement abundance using Poisson generalized linear regression models. Sexes were modeled individually given the potential for differential responses to invasive plants, resulting in four models. The vegetation layer (cover and underlayer) was also included as fixed effects, while plot was treated as a random effect nested within field.

Four additional Poisson models were created using selected vegetation covariates based on field observations of habitat use and presence both within and between plots. Forage grasses were included as they are the primary nesting strata for Bobolinks (Renfrew et al. 2020). Reed canary grass was included as it is a major component of hayfields and forms dense monocultures which discourage Bobolink nesting (N. Perlut unpub. data). Smooth bedstraw was chosen due to its prevalence in plots and its tight, knotted growth which may impair fledgling movement. Thatch was included due to its prevalence in the underlayer and importance as nesting substrate. The vegetation layer (cover and underlayer) were included as fixed effects, and plot was once again treated as a nested random effect within field.

Pooled (indicated by parentheses) Invasive model

Bird abundance = (reed canary grass + smooth bedstraw + knapweed) + thatch + layer + (plot/field)

Selected vegetation model

Bird abundance = forage grasses + reed canary grass + smooth bedstraw + thatch + layer + (plot/field)

To model how bird abundance changed between the initial and post-settlement surveys, the difference in maximum bird abundance between the two rounds of surveys and selected vegetation covariates were compared by linear regression; a Gaussian distribution was used to model these differences because negative values (which represents an abundance decline between the first and second round of surveys) are not suitable for a Poisson distribution.

Package *performance* (Lüdecke et al. 2025) was used to calculate the conditional R^2 value of each model, as well as to check for multicollinearity using the check_collinearity function. Nonparametric residuals fitted vs. simulated dispersion and zero-inflation tests were conducted using functions testResiduals and testZeroInflation in package *DHARMa,* and QQ plots were inspected (Hartig et al. 2024). When an initial model failed diagnostics, the model was rerun using a quasi-Poisson distribution (Ver Hoef and Boveng 2007) with vegetative covariate values that were grand mean centered and scaled to one standard deviation and then diagnostics were reassessed.

Results

Non-native species were the dominant vegetation encountered in fields, with native species comprising an average of just 2.5 ± 3% of dominant vegetation cover (Figure 1A), with the most common species being *Rubus* sp. and *Solidago* sp. Forage grasses comprised at least 50% of vegetation cover at 9 of 13 sites (62.9 ± 26.1% [SD], n = 13; Figure 1A). Other major components of the vegetation cover were smooth bedstraw (11.2 ± 9.9%; Figure 1A) and non-native legumes, primarily red and white clover (*Trifolium* sp.), bird's-foot trefoil (*Lotus corniculatus*), and tufted vetch (*Vicia cracca*; 5.4 ± 8.3%; Figure 1A). Spotted knapweed (*Centaurea* sp.) only comprised >1% of cover in two plots but it was a major component in those plots (17.6 ± 2.8%; Figure 1A).

While the underlayer vegetation was primarily composed of forage grasses (44.8 ± 12.8%; Figure 1B), smooth bedstraw (8.5 ± 5.1%), and legumes (5.4 ± 6.3%), thatch (22 ± 15.6%) and soil and moss (combined; 6 ± 2.2%) were also major structural components. Native species were more common than in the cover layer (6.1 ± 5.6%), mainly consisting of small species such as wood sorrels (*Oxalis* sp.), strawberry (*Fragaria* sp.), and meadow anemone *(Anemonastrum canadense*).

In general, more male Bobolinks were detected than females. During the first round of surveys the mean maximum number of females per one hectare plot was 1.9 (± 1.2), compared to 4.8 (± 2.2) for males. Abundances increased non-significantly during the post-settlement surveys for both females (2.3 ± 1.3) and males (4.9 ± 2.6).

When all invasive species were pooled together, there were no significant relationships with males or females during initial (respectively: Table 1, $R^2 = 0.34$; Table 2, $R^2 = 0.27$) or post-settlement (respectively: Table 3, $R^2 = 0.57$; Table 4, $R^2 = 0.37$). When modeled against selected vegetative covariates, reed canary grass was positively, significantly correlated with male ($\beta = 0.02 \pm 0.01$, $z = 2.01$, $P = 0.04$, $R^2 = 0.36$; Table 5) and female abundance ($\beta = 0.03 \pm 0.02$, $z = 1.98$, $P = < 0.05$, $R^2 = 0.28$; Table 6) during initial settlement. During the post-settlement period, the significant relationship with reed canary grass only persisted for females ($\beta = 0.03 \pm 0.02$, $z = 1.96$, $P = < 0.05$, $R^2 = 0.36$) (Tables 7 and 8).

Subsequent nonparametric dispersion tests and inspection of QQ plots showed that the female selected vegetation initial settlement model had heavy-tailed distributions which deviated significantly from the expected distribution ($P < 0.01$) and was zero-inflated ($P < 0.01$). When covariates were scaled and the selected vegetation initial settlement combined sex model was rerun with a quasi-Poisson distribution, it resulted in nonsignificant data dispersion ($P = 0.99$), though zero-inflation remained present ($P = 0.03$), even when a zero-inflation term was added; none of these vegetative covariates had a significant relationship with abundance ($R^2 = 0.16$; Table 9).

Severe variance inflation was not present in any of the pooled invasive models (VIF ≤ 3), but moderate variance inflation (VIF ≤ 9) was present in the selected vegetation models.

Discussion

Impact on Bobolink Abundance

While there was a marginally significant positive association between the abundance of males early in the season and percent of reed canary grass, it does not appear to be biologically meaningful past a density of ~25% reed canary grass (Figure 2). Reed canary grass thrives in the same moist portions of field where dense forage grasses and sedges would otherwise provide high-quality nesting habitat. As such, the positive association may be related to soil moisture, and is not necessarily direct evidence of a positive relationship between reed canary grass and bird abundance. Reed canary grass also rapidly grows tall, potentially providing attractive habitat earlier in the season when Bobolinks first arrive. Additionally, wet areas can provide high-quality foraging habitat for grassland birds (Wittenberger 1980), so these survey results may not be reflective of nest locations.

Though reed canary grass is not generally used for nesting, there may be benefits to its presence within a territory. Male Bobolinks frequently display from tall grass perches, and because reed canary grass grows tall and sturdy, it may provide an attractive perch for territorial defense. Additionally, though Bobolinks appear to require grasslands of at least 50-75% forage grasses, the patchy growth of reed canary grass may allow for areas of forage grass to persist, particularly in areas of elevated microtopography, which may explain why female abundance was positively correlated with reed canary grass during the nesting period.

Bobolinks have a polygynous breeding system with males having up to four mates (Martin 1971) and extra-pair copulations are common (Gavin and Bollinger 1985). This mating system allows for greater densities of females in high quality habitat where ample food for fledglings is available (Wittenberger 1980). Polygyny is most common on territories in wet (but not flooded) portions of fields, presumably due to the relationship between soil moisture and vegetation attributes as denser vegetation is associated with wetter substrate and moist pockets caused by microtopography result in better nest concealment (Martin 1971, Wittenberger 1980). Past studies have shown that the number of mates a male has is positively correlated with the density of protective vegetation cover within his territory, such as forbs and sedges in moist areas, whereas territories held by monogamous individuals had higher levels of short, patchy grass growing on drier ridges (Martin 1971).

The placement and size of territories held by male Bobolinks are a function of field size, edge type, and habitat quality (Fletcher and Koford 2003, Diemer and Nocera 2014). Polygynous males in high quality habitat tend to have smaller territories, thus density increases not just with field size (Vickery et al. 1994), but also field quality. These small, core territories tend to be held by older individuals, while younger individuals use larger territories on field peripheries, which are thought to be lower-quality (Nocera et al. 2009). As such, managing fields to promote high-quality vegetation structure could promote larger breeding populations.

Smaller territories tend to have higher abundance of arthropod prey items and greater vegetation height, density, litter depth, and ground cover (Diemer and Nocera 2014). Greater food availability may be necessary to allow non-primary females to successfully fledge young by compensating for the absence of male parental involvement in food provisioning (Martin 1974). Additionally, since movements of young are limited during the first five days post-fledging, greater food availability may be important for recently fledged young (Wittenberger 1980). If reed canary grass invasions further reduce food availability compared to forage grasses, invaded fields may become primarily used by unpaired males and monogamous breeding pairs.

Similar to our surveys, a past study found no impact of forb density on Bobolink density (Scheiman et al. 2003), though the territories of mated males have also been observed having significantly higher forb cover than unmated males (Wittenberger 1980). The mean density of forb cover in our plots (23.1 ± 15.9% (n = 13); 20.6 ± 13.5% non-native species, 2.5 ± 3% native) was similar to Scheiman et al. (2003), whose sites contained 5.6 ± 11.8% invasive leafy spurge (*Euphorbia esula*), and 13 ± 20% non-leafy spurge forb. It is possible that neither study had sufficiently high densities of forbs to surpass the theoretical threshold where Bobolink occupancy becomes untenable. The two plots in our study with the highest density of non-native forb (36.4 and 49.4%) had the lowest mean abundance of both females (1 per plot) and males (3 per plot). Conducting surveys in more plots composed of >50% non-native forbs may yield further insights into thresholds that prevent Bobolink settlement.

Grasslands with substantial forb encroachment may impact the breeding success of Bobolinks in ways which are distinct from the direct loss of forage grasses. Females tend to build nests at the base of large, stemmed, irregularly-spaced forb species that form an overstory above a layer of graminoids. These forbs provide shade and concealment, particularly early in the breeding season before graminoids have fully grown. However, some forbs that are common in Vermont’s hayfields, such as the native common goldenrod (*Solidago canadensis*), provide poor nesting cover compared to the less common golden Alexanders (*Zizia aurea*) and meadowrue (*Thalictrum* spp.) (Martin 1971). Clovers (*Trifolium* sp.), a commonly planted non-native fodder plant, also appear to provide suitable nesting cover for Bobolinks (Renfrew et al. 2020), though clovers can be outcompeted and replaced by other, more aggressive forbs.

Though changes in vegetation structure from forb encroachment may be similar between natural and anthropogenic hayfields, the factors impacting bird occupancy and survivorship, likely differ. Invasive species have impacts other than shifting and homogenizing the vegetation structure. For instance, though birds may readily nest in anthropogenic grasslands, nestling and post-fledging survival has been shown to be comparatively lower, potentially due to increased predation in their study systems (Lloyd and Martin 2005, Fisher and Davis 2011).

Several factors facilitate the ability of invasive plants to replace forage grasses. In native grasslands, invasive plants can rapidly alter the biotic (Gibbons et al. 2017) and chemical (Cappuccino and Arnason 2006) properties of soil by releasing allelopathic chemicals that hinder the growth of other species, as well as anti-herbivorous and anti-fungal chemicals (Cappuccino and Arnason 2006). Invasive plants require lower levels of macronutrients to thrive, such as phosphorus (Scharfy et al. 2011, Tang et al. 2025), which soil samples have shown is below recommended levels in many Vermont hayfields (K. Tolan unpub. data). Invasive plants also tend to exhibit a priority effect, where they produce seeds earlier in the growing season and are thus able to outcompete native species (Dickson et al. 2012).

The most problematic invasive species are classified as strong invaders, those which dominate communities (Ortega and Pearson 2005). One such species is spotted knapweed; while only present in two plots from the same field, they were major components and have become more dominant in the year since data collection since the field has remained largely uncut. The plots with knapweed also had the lowest density of forage grasses and fewest Bobolinks. Arthropod biomass decreases following the invasion of spotted knapweed in native prairies (Foster et al. 2021), however this decline may be less pronounced in non-native anthropogenic grasslands. Many of these strong invaders are adapted to warmer and drier conditions (Christina et al. 2023), and their spread is facilitated through changes in land use and fragmentation (e.g., along roadways (Gieselman et al. 2013)) and field edges (Holway 2005)).

While most observed species of plant were fairly common and easily identifiable in the field, there were several taxa where the species grouping designations may not be entirely accurate. For instance, goldenrods (n = 134) and many asters (family: Asteraceae, n = 134), except Knapweed (n = 209), were assumed to be native species. Similarly, the native meadow anemone (*Anemonastrum canadense*, n = 26) looks similar to largely non-native buttercups (*Ranunculus* sp., n = 1), when not in flower. That being said, the number of points that these potentially confusing species were observed at is negligible to the overall number of vegetation data points.

Research on the impact of forbs on grassland birds in northeastern grasslands is complicated by the fact that very few of these grassland ecosystems are naturally occurring. As such, studies on the impact of invasive plants on native grasslands likely do not translate to Northeastern anthropogenic hayfields. However, the response of birds to an invasion of forbs is likely similar between native and non-native grasslands as both undergo a similar change in the vegetation structure that drives Bobolink nest site selection (Sample and Mossman 1997, Nocera et al. 2007). While non-native grasses may have fewer, and less diverse arthropods (Andersen et al. 2019), birds breeding in anthropogenic grasslands do not appear to be limited by food availability (Zalik and Strong 2008, Dohms 2011) and grassland birds readily nest in non-native grasslands provided the structure and management is suitable (Lloyd and Martin 2005, Jones and Bock 2005, Perlut et al. 2006, Andersen and Steidl 2020).

Management Implications

The early detection of invasive plants is among the primary strategies to conserving global biodiversity (Welch 2014). Doing so allows for timely management to occur prior to a major invasion, significantly reducing the costs associated with invasive removal (Office of Technology Assessment 1993). In grasslands, the early detection of undesirable plants allows for targeted, relatively inexpensive management to prevent the entirety of the field from becoming unsuitable breeding habitat. In addition to proactively monitoring vegetation through ground-based surveys, especially along field margins, there have been successes using unmanned airborne craft and machine learning to monitor invasive plants (Singh et al. 2024), including spotted knapweed (Baron and Hill 2020), poison parsnip (Liu et al. 2021), and reed canary grass (Yoshitoshi et al. 2024).

Under current best management guidelines, landowners enrolled in programs such as NRCS' (Natural Resource Conservation Service) EQIP (Environmental Quality Incentives Program) and the Bobolink Project are unable to cut their fields before between 1 June and 1 August and 15 July, respectively. While this management regime conserves breeding habitat during the nesting season to reduce direct nest mortality, it also allows invasive plants to become established when they are left to seed freely. Over time, these invasive plants can dominate the field, which may render it unsuitable for nesting by ground-nesting grassland birds after a certain point. Rotational invasive plant management is one proposed method to manage grassland habitat. This strategy involves intensive invasive plant management on a portion of the field while delay mowing the rest; frequent cuts for several years can deplete the seedbank of invasive plants by preventing them going to seed, thus reducing their density and allowing for grasses to grow in. In theory, this plant management would facilitate both grassland bird breeding (in the unmowed portion) and management of invasives in sections of the fields that where frequently cut. Every few years, the portion of under invasive plant management would be switched.

Using soil amendments can be beneficial in ensuring forage grasses are not outcompeted by invaders. Many fields sampled in Vermont were below recommended levels of four macronutrients: calcium, phosphate, potassium, and nitrogen (K. Tolan unpub. data). Many invasive species require lower levels of macronutrients to thrive (Scharfy et al. 2011, Tang et al. 2025), so they are able to persist in nutrient-depleted soil after years of hay harvest. Wood ash has been found effective in reducing yellow rattle (*Rhinanthus minor*) invasions and restoring forage grasses such as timothy (*Phleum pratense*) and orchard (*Dactylis glomerata*) grasses, presumably by increasing pH and/or providing an injection of potassium (Eaton et al. 2017).

The twice-cut management strategy was developed in Vermont to reduce financial losses associated with grassland bird management that results from low frequency haying and low forage quality (Perlut et al. 2011), but may also reduce the rate of invasion by non-forage grasses that grassland birds avoid for nesting. Cutting earlier than 27 May could reduce the vigor of invasive species and delay flowering, with a subsequent second cut after ~65 days potentially doing the same later in the season. Importantly, cutting early in the season also allows enough time for grass to grow back to such a height where it is able to provide nesting habitat. However, this regime does not appear to facilitate renesting in other regions, such as Ontario, due to climatic limitations on cutting in mid-May (Diemer and Nocera 2016), and as such would likely be an issue outside of the Champlain and lower Connecticut River Valleys in Vermont. These limitations reduce the opportunities to manage grassland bird nesting habitat and invasive plants simultaneously. In regions where twice-cut management proves effective, there may be several benefits to it over once-cut "delayed" management in addition to reducing invasive species. Landowners are having an increasingly difficult time finding a farmer willing to delay hay, and more commonly need to pay a farmer to cut their field, or their field will go unmanaged. Higher nutrient content may make forage more attractive to farmers, helping to ensure fields are cut annually.

CHAPTER II: POST-FLEDGING BOBOLINK SURVIVAL IS POSITIVELY CORRELATED WITH MASS AND FLEDGE DATE

ABSTRACT

Forty-six Bobolink were tagged with VHF transmitters as nestlings and subsequently radio-tracked during the post-fledging period – the period of highest mortality in many songbird species. I tracked their daily post-fledging movements, habitat use, and survivorship in 2023 and 2024. Tracked birds remained on study fields for an average of 46.2 ± 8.5 [SD] days, using areas that were disproportionately open and far from field edges. Daily survivorship was positively correlated with mass and fledge date, and the cumulative 21-day probability of survival was ~50% for a bird of average mass and fledge date. These findings highlight the importance of incorporating post-fledging ecology into grassland habitat management as part of long-term land management.

Introduction

Few studies have examined the factors that promote success during the period between fledging and undergoing natal dispersal, known as the post-fledging period (Morton et al. 1991, Cox et al. 2014). The week immediately following nest departure is a survival bottleneck marked by elevated levels of mortality for many altricial species (Cox et al. 2014, Naef-Daenzer and Grüebler 2016a, Jones et al. 2025), and can be the period of highest mortality throughout birds' lives, thus placing a theoretical limit on survivorship. Therefore, the integration of post-fledging ecology into conservation planning may have a substantial effect on population dynamics and conservation (Streby et al. 2014).

The number of days since fledging can be the most meaningful predictor of post-fledging survival in many songbirds, though daily survival appears to level off within 21 days of fledging in most species (Cox et al. 2014). Hatch date and body mass are also closely correlated with survival (Maness and Anderson 2013, Cox et al. 2014). Since habitat quality can affect body condition and mass (Wilkin et al. 2009), survivorship may be indirectly influenced by habitat features and quality (Cox et al. 2014). For example, distances moved by two warbler species (family: Parulidae) during the post-fledging period were positively correlated with nestling condition (Vitz and Rodewald 2010). Additionally, the development rate of wings and flight feathers in pre-fledged individuals has carryover effects on post-fledging survival rate (Jones et al. 2017, Jones and Ward 2020). Thus, poor nesting habitat quality may result in impaired flight and lower survival upon departing the nest.

Habitat use has been the most studied aspect of the post-fledging period in songbirds. In some species, habitat use shifts over the course of the post-fledging period; some migratory forest species use early successional habitat during the post-fledging period (Anders et al. 1997, 1998; Vitz and Rodewald 2006, 2007; Delancey and Islam 2019, Fiss et al. 2020), which may increase survivorship by offering protection from predation or a greater abundance of food (Anders et al. 1997, 1998; Vitz and Rodewald 2007). Although grasslands are less structurally diverse than woodlands, fine-scale variation in plant species composition, vegetation structure, ground cover, and moisture can affect habitat use patterns. Post-fledging Dickcissels (*Spiza americana*) that used denser habitat within the first three days of fledging had greater survival rates than those in less dense habitat (Jones et al. 2017), while Grasshopper Sparrows (*Ammodramus savannarum*) transitioned from denser vegetation to patchy vegetation to open habitats, which may reflect shifts in thermoregulatory and predator avoidance needs as they begin foraging for upon parental independence (Small et al. 2015). Eastern Meadowlarks (*Sturnella magna*) used comparatively more agricultural habitat during the post-fledging period than breeding individuals, potentially because prey availability was greater and/or predator abundance was reduced in these fields (Kershner et al. 2009).

The study of individuals during the post-fledging period is complicated by the difficulty of finding nests, as well as the elusive nature, low survivorship, and small body mass of recently fledged individuals, which historically rendered them unsuitable (or prohibitively expensive) for many types of tracking technology (Wikelski et al. 2007, Streby et al. 2014). However, technological advancements have allowed for in-depth tracking to occur for the duration of this period. Understanding the post-fledging patterns and survivorship can allow for informed management decisions to be made at spatial scales larger than a single breeding locale. This may be especially important for species which are subject to regular human habitat disturbances, such as grassland birds.

The Bobolink (*Dolichonyx oryzivorus*) is a long-distance migratory ground-nesting grassland songbird species that breeds throughout the northern United States and southern Canada, and overwinters throughout south-central South America (Renfrew et al. 2019). They exhibit high levels of breeding site fidelity (Gavin and Bollinger 1988), and adults that nest successfully are more likely to return to the same breeding field in subsequent seasons (Gavin and Bollinger 1988, Fajardo et al. 2009). Natal philopatry is also high, with ~30% of nestlings recaptured near their natal locale in subsequent years (Cava et al. 2016). In the northeast, Bobolinks nest predominantly in agricultural landscapes, and as such are heavily impacted by human management during the breeding season. Avoiding the direct destruction of nests by not haying during the primary nesting season (June and early-July) is a commonly used conservation strategy (Perlut et al. 2006). Long-term capture-mark-recapture studies indicate that Bobolink nestling mass is negatively correlated with apparent first-year survivorship (Perlut and Strong 2016), though this may be due to heavier nestlings dispersing beyond the study site, thus avoiding recapture. Lighter, late-hatching individuals are thought to disperse shorter distances, presumably since they do not have as much time before initiating autumnal migration to evaluate potential breeding sites for subsequent seasons. Subsequent studies have also shown that apparent first-year survival rates are highest in individuals that fledged earlier in the season from first nesting attempts (White et al. 2021).

While area sensitivity has been observed across a range of terrestrial taxa and biomes (Robbins et al. 1989, Benoit and Askins 2002, Desrochers et al. 2010, Ontario Ministry of Natural Resources 2019), its role in nest site selection has been extensively documented in grassland birds, with density and occupancy positively correlated with patch size in most species (Vickery et al. 1994, Johnson 2001, Ribic et al. 2009). While local populations vary, with fields larger than 10 ha supporting higher nesting densities than smaller fields (Norment et al. 1999). Bobolink have been shown to place nests disproportionately far from field edges (Bollinger and Gavin 2004) though, similarly to other area-sensitive grassland species (DeLisle and Savidge 1996), distance to edge does not appear to correlate with nesting success (Keyel et al. 2013). The impact of edges on nest placement differ by edge type, with woodlands (Fletcher and Koford 2003) and hedgerows (Perkins et al. 2013) showing the strongest impacts on nest placement. The avoidance of edges appears to compound when multiple edges meet, further impacting Bobolink nesting behavior in highly fragmented landscapes (Fletcher 2005). Landscape openness, a measure of visual obstruction to the horizon which is a function of distance to edge, edge height, and topography, can act as a proxy measurement for area sensitivity in grasslands (Renfrew and Ribic 2002). As such, openness has emerged proxy for grassland landscape suitability and appears to be a driver of nesting abundance for some grassland birds (Renfrew and Ribic 2002), in some cases more so than patch size (McDonald and Koper 2022).

To aid in the understanding of spatial use patterns, random walk models can be used to simulate and describe movement patterns (Kareiva and Shigesada 1983, Turchin 1998). These discrete probabilistic models describe movement through steps of underlying trajectories and turns, thus simulating idealized “walkers” which move across a simulated landscape. Composite Brownian walks (CBWs) mimic the realistic movements of wildlife by interspersing states of randomness with directionality, thus accounting for a variety of movement patterns such as foraging, transit, and resting (Benhamou 2007, Jansen et al. 2012, Reynolds 2014, Benhamou and Collet 2015, Ando et al. 2022).

Utilizing miniature nanotags and telemetry, we studied the movements and survivorship of post-fledging Bobolink, and the relative impact of two landscape attributes. Our goals were to 1) calculate post-fledging survivorship as a function of mass, fledge date, fledge year, natal site management regime, and days post-fledging, 2) assess the relative importance of openness and distance to edge on post-fledging occurrence, and 3) compare the post-fledging habitat use of tracked birds versus simulated random walkers.

Methods

Fieldwork

Study sites

Research was conducted on Shelburne Farms, a working educational farm located in Shelburne, Vermont (44.3921, -73.2572) whose landscape is dominated by hayfields separated from one another by gravel roads and small woodlots (Figure 2). Four primary study fields were used in both 2023 and 2024. Two 15-hectare fields, Windmill Hill (WH) and Stern (hereafter "twice-cut"), were hayed once on 16 or 17 May in 2023 and 2024 and again on 26 July (2023) and between 3 and 6 August (2024). The other two primary deployment fields (Harris [18 ha] and Elm Marsh [EM, 16 ha]; hereafter "once-cut") went uncut during the main nesting period (May through 1 August) of both years. Two additional fields (Sadler [10 ha] and Dixon [5.5 ha]), which were only used for deployment in 2023, were hayed on 6 July (hereafter "mid-season cut").

Study design

Between May and July in 2023 and 2024, field crews searched for Bobolink nests by flushing incubating females off their nests and through observing adult nesting behaviors. Nests were monitored every 1-2 days, which included measuring nestling body mass once at eight or nine days after hatching. Immediately after weighing, Lotek NTQB2-3-2 Coded VHF Nanotags were affixed using backpack-style leg loop harnesses (Rappole and Tipton

1991) to up to four randomly selected nestlings per nest prior to fledging. Harnesses were made from 0.7 mm diameter Stretch Magic® elastic silicone cord. All tags and harnesses weighed less than 3% of a nestling's total body mass.

Post-fledging movements and survivorship of tagged birds began following the deployment of nanotags. Fledglings were tracked using a hand-held Lotek Biotracker VHF Receiver and a directional tri-element folding Yagi antenna. Individuals were approached on foot, flushed, and confirmed visually when possible. In 2023, there was no telemetry data collected between 13 and 21 July, and limited data were collected after 18 August. In 2024, daily location fixes were obtained for each individual until death or natal dispersal beyond the study area. In most cases, GPS fixes were taken within 5 m of where the bird had been prior to being flushed.

A LiDAR-derived 0.35 m^2 digital elevation model (Vermont Center for Geographic Information [VCGI] et al. 2023) was used to calculate landscape openness (Keyel et al. 2013, Allen et al. 2022) utilizing the *rgrass* package (Bivand et al. 2024) to interface with the GrassGIS program (GRASS Development Team et al. 2024) and r.skyview's openness function (Yokoyama 2002, Zakšek et al. 2011, Petrasova 2022). Openness (% of horizon visible at each raster cell) was calculated in 16 directions from each cell, then averaged to calculate each cell's mean openness and multiplied by 0.9 to convert from percentage to angle in degrees. The distance to closest field edge (m) of each point was calculated using a vector agricultural lands dataset (University of Vermont Spatial Analysis Laboratory 2022). Several polygon edges were altered to better reflect field observations: an unused, grown-over farm road was removed as an edge from the spatial dataset, and a hedgerow was digitally added that separated two adjacent fields.

Analysis

Movement

GPS locations from telemetry fixes were brought into R using package *sf* (Pebesma 2018) for vector data and either *terra* (Hijmans et al. 2025a) or *raster* (Hijmans et al. 2025b) for raster data.

Survivorship

I created seven models describing daily survivorship of Bobolinks within the first 31 days post-fledging, roughly 10 days longer than the period of parental dependence and prior to any individuals dispersing from the study site. As an initial exploratory analysis, one intercept-only and five univariate models were created using five variables: nestling mass at time of tagging, date of fledging, field management regime, year, and days post-fledging. Models were compared using Akaike's information criterion corrected for small sample sizes (AICc). Year- and management-only models both performed worse than the null model, and thus were excluded from subsequent multivariate models. Days post-fledging was also omitted from multivariate analysis as it is a time-varying covariate, and as such was not included in time-constant models. Pollock's staggered Kaplan-Meier known-fate candidate models (Kaplan and Meier 1958, Pollock et al. 1989) were created using *Program MARK* (White and Burnham 1999) in the R (R Core Team 2024) *RMark* package

(Laake 2013). Two individuals were excluded because we lacked mass measurements for them. Ordinal day (the number of days since 1 January of the respective year) was used to represent dates to account for 2024 having been a leap year; in cases where dates are provided, they are based on the non-leap year calendar. Results are reported with standard error.

Habitat use

Four binomial generalized linear models were created in *glmmTMB* (Brooks et al. 2017) to compare the relative effects of mass, distance to edge, and openness on fledgling occupancy. The openness raster was aggregated from 0.35 m^2 to 25.2 m^2 and each cell's distance to closest field edge was calculated. Each cell was assigned a binary value indicating the presence/absence for each bird (1 = detected using that cell), for the maximum number of days an individual was detected (one through 44). Openness, distance to edge, and mass at time of fledging were grand mean centered and scaled to one standard deviation, and included as fixed covariates. Band number was included as a nested random effect within nest identifier. To account for potential temporal autocorrelation, days post-fledging was included as an autoregressive AR1 term. A global model with all three covariates, and three partial models of covariate combinations, were compared using Akaike's information criterion corrected for small sample sizes (AICc). Results are reported with standard error.

Composite Brownian walks with a maximum step length of 58 m (the median distance between subsequent fixes of tracked birds) were simulated in the package *SiMRiv*

(Quaglietta and Porto 2019, 2024). Given the heavy positive skew of distances between subsequent fixes (sk = 5.9), median distance (58 m) was chosen as maximum step length rather than the mean (124 m). Additionally, this step length is less than the width of the polygons that represent grasslands, a requirement when using *SiMRiv*. Five iterations of 400 steps were simulated for each nest location and resampled every 10 steps to reduce spatial autocorrelation (Kareiva and Shigesada 1983, Turchin 1998, Quaglietta and Porto 2024). Prior to each step calculation, walkers in the Brownian Walk (BW) state had a 0.5% chance of transitioning to a correlated random walk (CRW), and a 10% chance of transitioning from CRW to BW. These likelihoods help simulate the behaviors of localized (BW) and inter-field (CRW) movements. Net squared displacement (NSD; the absolute Euclidean distance between an organism and its natal site) was calculated at each timestep for individuals using the R package *amt* (Signer et al. 2024). Simulated walker movements were not spatially limited by the simulated landscape as no individuals reached the edge of available space. Both distance to edge and openness were compared between telemetry tracks and simulated paths using generalized linear models in *lme4* (Bates et al. 2025), with nest, field, and year included as nested random effect variables.

Results

Movement

Between June and August of 2023 and 2024, 46 Bobolink nestlings from 29 nests were tagged and subsequently tracked in Shelburne, Vermont (Figure 2), generating 795 location fixes (Figure 3). Post-fledging Bobolinks used the same habitat as nesting adults, remaining in hayfields for the entirety of the tracking period. The average absolute Euclidean displacement distance (distance from natal nest) did not reach 100 m until nine days post-fledging (n = 27). The mean linear distance between daily telemetry fixes (step length) was 33.6 m (± 3 m, n = 232) through nine days post-fledging. In the week following this period (days nine through 15 post-fledging) the mean step length was 88 m (± 7.05 m, n = 148). After day 15, the mean step length increased to 224.5 m (± 17.2 m, n = 320).

Movements away from the nest within the 21 days post-fledging were restricted relative to subsequent movements (Figure 4A). During the first 21 days, the Euclidean distance individuals moved from the nest increased linearly by 11.6 ± 0.5 m ($R^2 = 0.96$, $z = 22.4$, $P < 0.001$), while between days 21 and 31 the distance increased by 32.5 ± 5.3 m ($R^2 = 0.77$, $z = 5.87$, $P < 0.001$) per day. The distance between telemetry fixes did not follow the same pattern; in the first 21 days, the daily travel distance increased linearly by 6.8 ± 0.4 m ($R^2 = 0.92$, $z = 15.5$, $P < 0.001$; Figure 4B), while a non-significant linear relationship existed between days 21 and 31 ($\beta = 7.3 \pm 4.4$, $R^2 = 0.24$, $z = 1.7$, $P = 0.13$).

While birds remained in grassland habitat throughout the post-fledging period, movements between fields tended to coincide with haying. Shortly after mowing on a twice-cut field in 2023, three birds moved to a 4.5 ha field separated by ~100 m of forest (at 16-, 19-, and 37 days post-fledging). In 2024, three birds from that field moved to a 10-ha hillside field directly east that was cut 41 days prior, separated by a dirt road and small hedgerow (at 19-, 23-, and 23 days post-fledging).

Two birds, which dispersed on 8 August and 13 August from a once-cut field, relocated to a separate once-cut field at 37- and 50 days post-fledging, respectively. A third individual that fledged from a middle-cut field and was displaced on 12 July (20 days post-fledging), shortly following management, was detected in a once-cut field on 22 July, before departing on 9 August (48 days post-fledging) to the other once-cut field. One individual traveled between the adjacent twice-cut Harris and Stern fields at 7 days post-fledging; other birds from those fields first transited between on days 10-, 10-, 11-, 20-, and 20 post-fledging.

One particularly mobile individual departed a twice-cut field after 18 days post-fledging and was not detected again until day 25 post-fledging on a once-cut field (EM), separated from its natal field by 1.2 km. Upon departing EM at 35 days post-fledging, it was detected 1.3 km away on day 40 on its natal field.

Survivorship

Seven birds were presumed to have successfully dispersed from the study fields in both 2023 and 2024 (35% and 39% of tagged birds, respectively), remaining on the fields until 46.2 (± 8.5 [SD], n =14, range: 31 – 63) days post-fledging, after which they were not detected within the study site. The earliest dispersal from the study site occurred on 8 August and the latest on 26 August. This is likely earlier than actual dispersal, particularly in 2023, when no telemetry occurred after 26 August.

Daily survival did not meaningfully differ between the once-cut and twice-mowed field (AICc Δ19.9), however more individuals successfully fledged from twice-cut fields than those only cut once. Twice-cut fields successfully fledged 10 young (50% success rate), once-cut fields successfully fledged three individuals (15% success rate), and mid-cut fields only successfully fledged one individual (20% success rate). Of the five tags deployed on mid-season cut fields, the four birds that did not successfully disperse died within four days of fledging. The one bird that did successfully disperse from the mid-cut fields fledged on 22 June, the latest of the birds tagged on those fields, weighed 23.6 grams, more than two grams heavier than the next heaviest individual on the mid-cut fields.

Four mortalities were attributed to storm exposure as there was no visible physical damage to the recovered corpses, and the deaths occurred immediately following severe rainstorms. Four deaths appeared to have been caused, at least in part, by apparent entanglement of either the aluminum USGS band or nanotag. Four other individuals were likely depredated since their nanotags were retrieved and had tooth marks. The mortality of one free-flying fledgling (44 days post-fledging) was attributed to predation as the nanotag's signal was coming from the canopy of a forest edge for several days without moving, though that field had not been cut. Three tags in 2023 appear to have been attached too loosely and fell off.

The best supported model of daily survivorship (Table 10) included both mass at the time of tagging ($\beta = 0.44 \pm 0.14$) and fledge date ($\beta = 0.1 \pm 0.03$; Table 11), which were both positively associated with survivorship; nestling mass had a greater effect size than fledge date (odds ratios of 1.55 vs. 1.11, respectively; Table 11). When fledge date was held consistent, daily survival ranged from 0.85 ± 0.04 for an 18 g bird to $0.99 \pm < 0.01$ for a 24 g bird (Figure 5A). Birds that died weighed significantly less than birds that successfully fledged ($t = -14.6$, $p < 0.001$). The mean mass of nestlings that subsequently died during the post-fledging period was 20.4 g ($\pm$ 0.28, n = 31), while birds that successfully dispersed averaged 22.2 g ($\pm$ 0.45, n = 13; Figure 7); only one individual that weighed less than 20 g at the time of tagging successfully dispersed. No weight class that fledged on 12 June, the earliest date modeled, had a predicted cumulative 21-day cumulative survival probability of ≥ 0.5 (Figure 8). The survivorship of individuals that fledged in June was relatively low overall, as only individuals weighing > 22 g had a predicted 21-day cumulative survival probability of > 0.5. Conversely, all weight classes > ~18 g that fledged in July had a cumulative survival probability of > 0.5. When mass was held consistent to assess the impact of fledge date on survival, the lowest probability of *S* was estimated for birds that fledged on 13 June (0.8 ± 0.8), increasing to $\geq 0.93 \pm 0.01$ for those that fledged on, or after, 27 June (Figure 6B).

Survival increased over the course of the post-fledging period, though the number of days post-fledging was not a highly ranked predictor of survival (AICc Δ16.41). When looking at the 21-day period immediately following nest departure, the period of parental dependence in Bobolink and when movement away from the nest appear limited, the predicted daily survival surpassed 0.9 ($\pm$ 0.04) on day 8 post-fledging, with the 95% survival confidence interval being entirely above 90% after three weeks. While predicted daily survival surpassed 0.9 (95% CI: 0.79 – 0.96) within eight days post-fledging, the wide confidence interval shows uncertainty in this estimation.

Habitat use

Spatial use was best explained by the model which included mass, distance to nearest edge, and mean landscape openness as covariates (Table 12). In the best fitting model, openness ($\beta = 4.0 \pm 0.33$, OR = 54.49; Table 13) had a greater effect size than both mass ($\beta = 0.41 \pm .024$, OR = 1.51) and distance to edge ($\beta = 0.28$, OR = 0.04).

When compared with simulated walkers, tracked individuals used habitat with significantly greater landscape openness ($p < 0.001$, $t = 14.5$) and was farther from field edges ($p < 0.001$, $t = 15.2$). The maximum net square displacement, a frequently used metric to gauge the difference between real and simulated movements (Kareiva and Shigesada 1983, Turchin 1998), did not differ significantly between simulation and recorded telemetry movements ($p = 0.79$, $t = 0.27$), indicating that simulated movements occurred within a similar spatial range to the telemetric data.

Discussion

Movement

The average distance from nests and distance between daily locations both increased throughout the post-fledging period, contrasting with some other studies where fledglings settled into post-fledging home ranges (Anders et al. 1998, Styles et al. 2021, Mueller et al. 2025). The active management of our study sites likely prevented this from occurring in fields cut prior to September, the period that birds remained on the study fields, by forcing individuals to relocate earlier than they otherwise would have. Additionally, individuals dispersing through spaces away from their home range can exhibit greater rates of predation compared to individuals that remained on a single home range (Yoder 2004), which could impact birds on cut fields.

While birds hatched from twice-cut management were unable to remain on natal fields past mid-July, when haying occurred, birds in once-cut fields also relocated from their natal field to elsewhere on the study site prior to the onset of migration despite no management occurring. While the constant pressure of relocating fields during the post-fledging period may be detrimental to post-fledging survival, their flocking behavior and relatively similar behavior between management regimes could suggest a strategy of migratory staging that's relatively unimpacted by management activities.

One commonly suggested purpose of post-fledging movements is prospecting for future nesting sites; males of some songbird species establish their first breeding territory closer to where they spent the post-fledging period than their natal site, indicating that developing a level of familiarity to an area during the post-fledging period can be an important aspect of breeding site selection (Patchett et al. 2022). For species that undertake long-distance migration, individuals may also create regional-level mental maps to assist with navigation during the natal dispersal period, and potentially, subsequent migrations (Brown and Taylor 2015). As such, the movements documented may have been exploratory in nature. It has also been suggested that Bobolinks use social cues during the post-breeding season which influences subsequent breeding site selection (Nocera et al. 2006). Since Bobolink form mixed-age and -sex flocks after the breeding season, the young birds' movements might have been directed by adults in their flock.

The earliest an individual transited between non-adjacent fields was 16 days post-fledging, approximately the same amount of time it takes post-fledglings to gain full flight capabilities (Martin 1971). While an individual did move from Harris to Stern at 7 days post-fledging, the hedgerow that separates those two fields is < ~5 m in width and height. As such, even a newly fledged bird with relatively poor flight capabilities would be able to see over the hedgerow and move between fields. Of the individuals that moved between fields in response to haying, none were documented traveling >1 km immediately following management, highlighting the importance of suitable local habitat.

Survivorship

When daily survival is modeled as a function of days post-fledging, the period of highest mortality (95% CI > 0.9) coincides with the ~21 day period after departing the nest when movements were relatively restricted, as well as the period of parental dependance. This three week period corroborates others' findings (eg. Anders et al. 1998), and has been used as the period of comparison in meta-analyses (Cox et al. 2014).

The relationship between mass and fledge date appears to greatly impact survival (Figure 8). For instance, birds that weigh ~20 g had a cumulative survival rate of < 0.25 over the first 21 days post-fledging when fledging occurred prior to 1 July, which increased to > 0.5

fledged after 10 July. Conversely, birds that weighed > 24 g had a cumulative 21 day survival rate of > 0.25 regardless of fledge date, surpassing 0.75 by 30 June.

The positive association between mass and survivorship contrasts to a past study of apparent first-year survivorship of this Bobolink study population which found greater apparent survival of lighter birds (Perlut and Strong 2016). However, those results are likely influenced by heavier individuals dispersing further from their natal territory than lighter birds, making them less susceptible to recapture. The mass correlates positively with survivorship in many altricial songbirds (Maness and Anderson 2013, Naef-Daenzer and Grüebler 2016a), in some cases acting as a threshold under which individuals had 0% fledging success (Magrath 1991). Only one bird that weighed less than 20 g successfully dispersed from our study site, potentially hinting at the lower limit of mass which must be reached to successfully fledge. However, this pattern does not hold true for all species: the mass of fledging Eastern Meadowlark was not a significant driver of survivorship with mortalities tending to weigh more than survivors (Kershner et al. 2009).

A phenological trade-off has been observed between fledging early (when predation risks are lowest) versus fledging later (when food availability is highest; Naef-Daenzer et al. 2001), and invertebrate sampling done in prior years on two of the study fields showed invertebrate biomass peaks in July (Zalik and Strong 2008). Tracked birds that fledged in mid-June would have experienced lower levels of available prey items than those which fledged in subsequent weeks, as has been hypothesized in other species of grassland bird which display a similar trend (Yackel Adams et al. 2006, Fisher and Davis 2011). While provisioning rate and food availability has not been shown to directly impact nestling condition in grasslands (Zalik and Strong 2008, Kraus et al. 2025), birds that fledge earlier in the season may experience decreased food availability upon departing the nest which are not documented by studies during the nestling period.

An alternative explanation for the relationship between fledging date and survival is that individuals born later in the season were exposed to predators for a shorter period during the study as their tracking period was shorter. While some grassland birds use denser vegetation early in the post-fledging period, that ends once they gain flight abilities (Jones et al. 2017). Dickcissel used denser habitat through 11 days post-fledging, likely to facilitate predator avoidance and to avoid extreme weather (Jones et al. 2017). Similarly, Grasshopper Sparrows shifted from denser to sparser vegetation at 32 days post-fledging to facilitate foraging upon gaining independence (Small et al. 2015). One of the key defenses of free-flying Bobolink against predation is flocking. In such an open environment with minimal opportunities to use habitats which increase predator avoidance, predation risk may increase with time spent on the natal field.

The positive survival and fledge date relationship is not necessarily reflective of survival to breeding age. Birds on once-cut fields dispersed between fields at older ages than birds fledging from twice-cut fields. In Bobolinks, apparent first-year survival rates are highest in individuals that fledged earlier in the season, particularly those from first nesting attempts (White et al., 2021). Birds that fledged earlier in the season spent significantly more time on the study fields prior to dispersing than those born later in the season (z =

5.2, $p < 0.001$), meaning that birds fledging later in the season had less time to prepare for migration or prospect for future breeding sites (Wells et al. 2007). As such, there may be carry-over effects on post-dispersal survivorship that was not captured during this study since hatching later in the season can deprive birds from gathering the nutrient reserves necessary for migration (Dawson and Clark 2000). Additionally, birds that fledge earlier may have greater flight capabilities to avoid haying machinery on fields cut in early-July, which may benefit recruitment.

Though the overall survival rate did not differ between study years (ΔAICc = 18.81) and both years had similar levels of dispersal success, the temporal pattern of mortality differed. In 2023 ~50% (13 / 26) of mortalities occurred within the first three days post-fledging, whereas in 2024 it took 19 days post-fledging to reach the same ~50% (8 / 20) level of mortality, which may partially account for the poor predictive power of days post-fledging on survival rates. Lark Bunting (*Calamospiza melanocorys*) and Dickcissel (*Spiza americana*), both midwestern grassland species, had lower daily survival within the first three days post-fledging (Yackel Adams et al. 2006, Wells et al. 2007) (Yackel Adams et al. 2006, Kershner et al. 2009), whereas it took eight days for our tracked birds to surpass 0.9.. Eastern Meadowlarks (*Sturnella magna*) exhibited a similar trend, with 90% of mortality occurring within the first week of fledging (Wells et al. 2007).

Habitat use

Openness impacted habitat use more than distance to edge (Table 13), with individuals occupying habitat with a mean openness of 81° (± 0.1, n = 746) at a mean distance to edge of 89.2 m (± 1.8). Nearly all locations (97%) occurred in habitat with a mean openness of > 0.7 (n = 722). This is similar to the breeding habits of Bobolink, which appear to disproportionately nest in portions of fields with a mean landscape openness of at least 80º, and openness explains nest placement (Keyel et al. 2012) and breeding densities (McDonald and Koper 2022) better than field size or distance to edge.

There are several proposed drivers of edge avoidance and area sensitivity, with one of the primary ones put forth being the reduction of predation risk perception in open landscapes (Lima & Valone, 1991) since birds disproportionately nest in more open areas, away from predators nests (van der Vliet et al. 2008). Though Bobolink nestling survival does not appear impacted by either openness or distance to edge (Keyel et al. 2013), the impact of openness on survival may increase upon fledging and increasing self-reliance when individuals are more responsible for predator avoidance than during the nesting period.

Conclusion

An apparent tradeoff exists in Bobolink between breeding early, potentially providing more time to prepare for natal dispersal (Naef-Daenzer and Grüebler 2016b, White et al. 2021), and breeding late, when food items are most abundant and post-fledging survival is highest. That apparent first-year survival found the opposite effect of body mass (Perlut and Strong 2016) and fledge date (White et al. 2021) is challenging to reconcile with these results. With technological advances, such as the Motus network of automated telemetry towers, we may be able to look beyond the confines of the study site and provide a more holistic understanding of the factors that impact their first-year return rate. Since the post-fledging period is a time of high mortality and is frequently influenced at a smaller spatial scale than other periods of a bird's lifecycle (Cox et al. 2014), improving the survival of birds during this period, particularly during the three weeks immediately after departing the nest, may have a dramatic impact on localized population recoveries. Given the intercontinental migratory nature of Bobolinks, and their heavily managed breeding grounds, a more thorough understanding of first-year survivorship may facilitate increased reproductive success.

Body condition and mass can be a function of habitat quality (Wilkin et al. 2009), so survivorship can be indirectly influenced by habitat features (Cox et al. 2014). In addition to daily survival being positive correlated with mass, so too was habitat use, indicating that heavier birds were more likely to survive. Assessing the impact of different vegetation types and management strategies that increase nestling mass may facilitate higher levels of post-fledging survival.

As nesting and post-fledging Bobolink disproportionately utilize field interiors, timely control of invasive plants can reduce the impact that invasive plants have on breeding birds when plants are prevented from spreading into field interiors. Additionally, the impact of invasive vegetation on food availability compared to non-native forage grasses remains unknown. There is a pressing need for flexible grassland bird-friendly management strategies that simultaneously protect suitable nesting habitat while also reducing the inundation by invasive species. Additionally, bird-friendly management which can also produce nutrient-rich forage may reduce the financial loss associated with grassland bird conservation, aiding in the long-term maintenance of suitable habitat. Since post-fledging survival is positively correlated with fledge date, a two-cut management strategy might produce young during the period which facilitates higher post-fledging survival, though the effects on natal dispersal and first year success remains unknown.

Figures and Tables

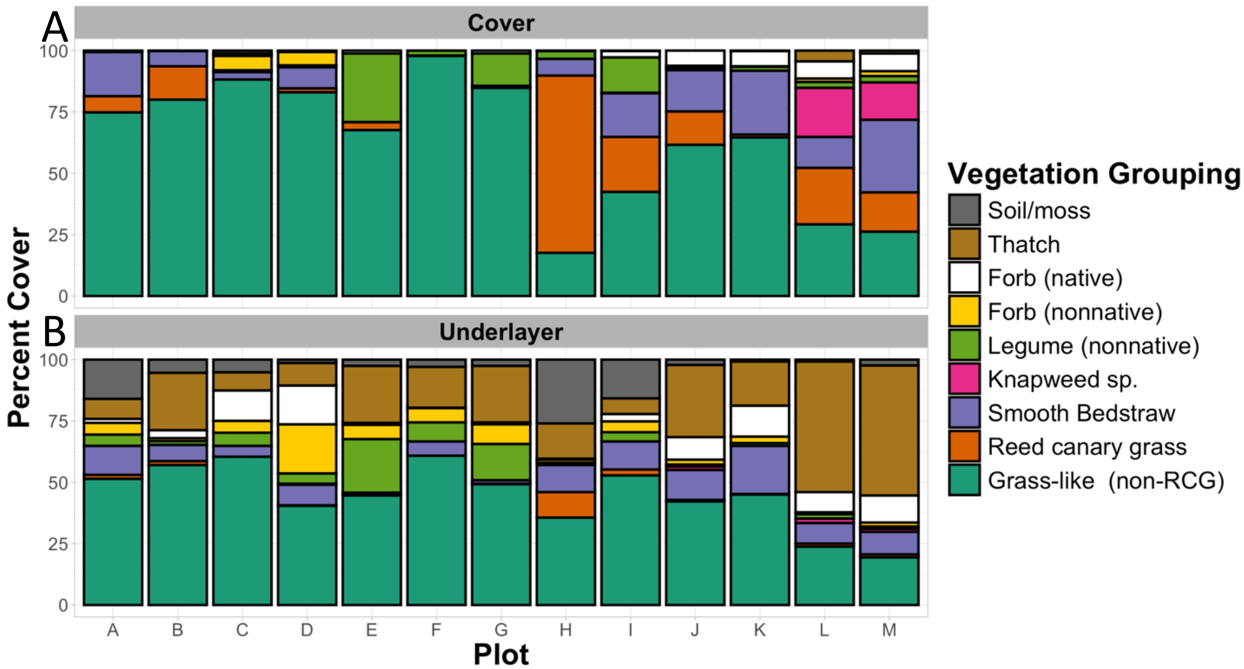

Figure 1. The vegetation composition from 500 point samples taken in each of 13 one-hectare plots. A: The dominant vegetation within a 15 cm radius of each sample point. B: The plant species directly rooted at each sample point.

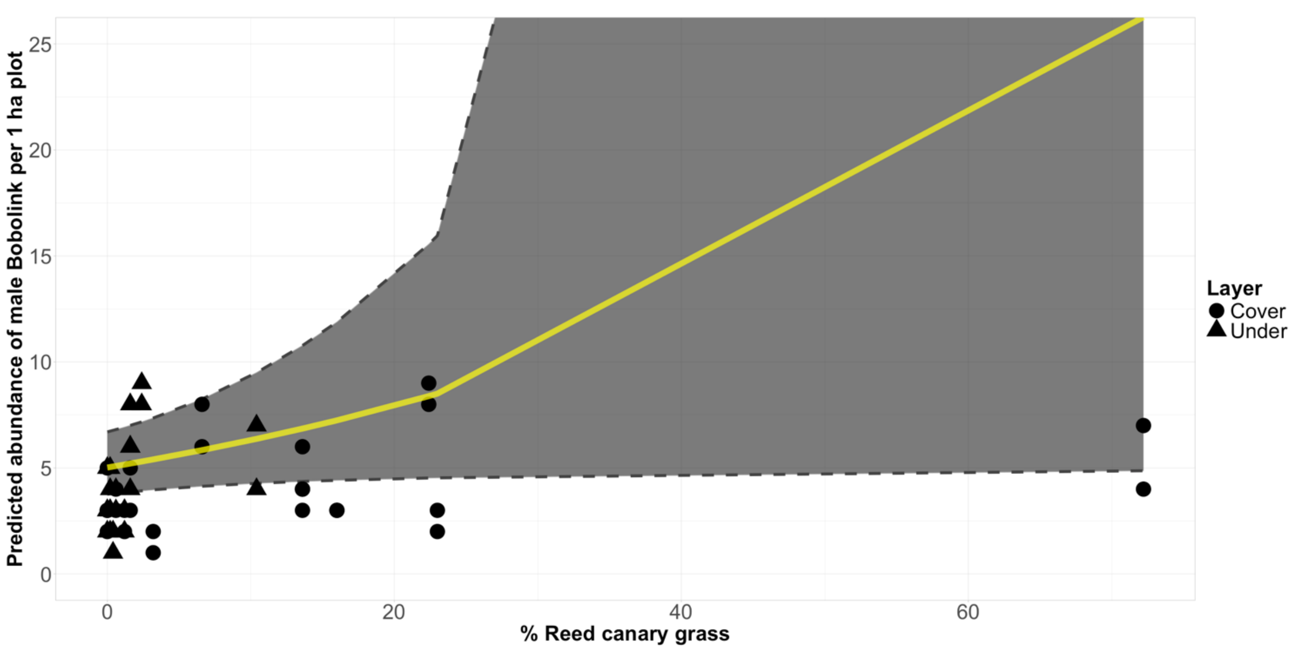

Figure 2. Predictions from the regression model from Table 5 of male adult Bobolink abundance as a function of reed canary grass. Points indicate corresponding bird

abundances and reed canary grass from survey plots. The gray region indicates a 95% confidence interval.

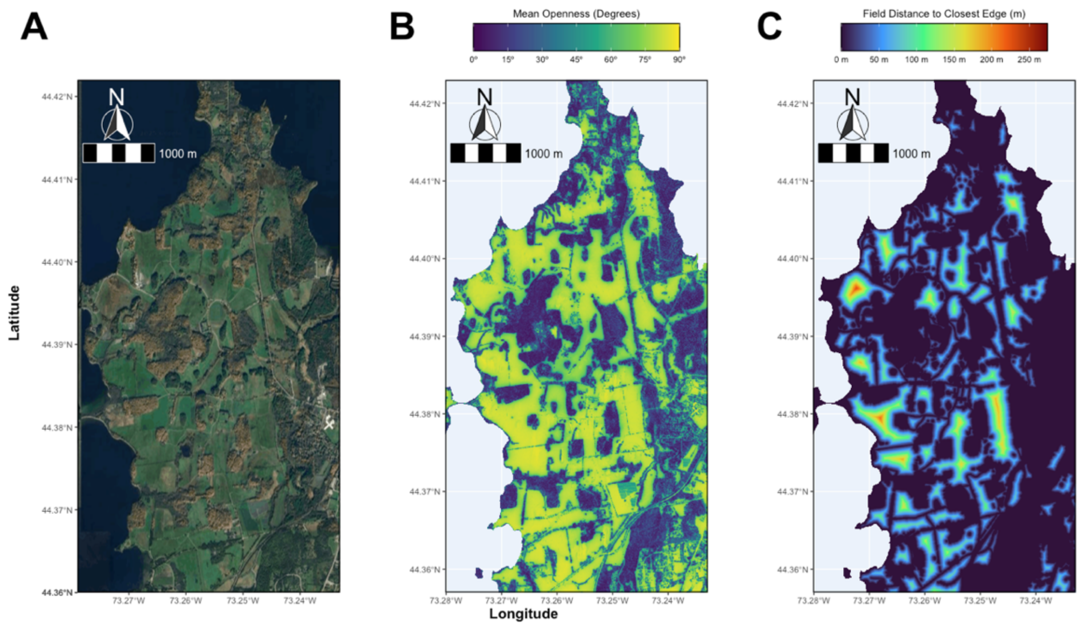

Figure 3. A: Satellite image of the Shelburne Farms study site. B: Mean openness of each 0.35 m^2 raster cell of the Shelburne Farms study site. C: Minimum distance of open areas to forest of the Shelburne Farms study site. Note: non-grasslands have a distance of zero.

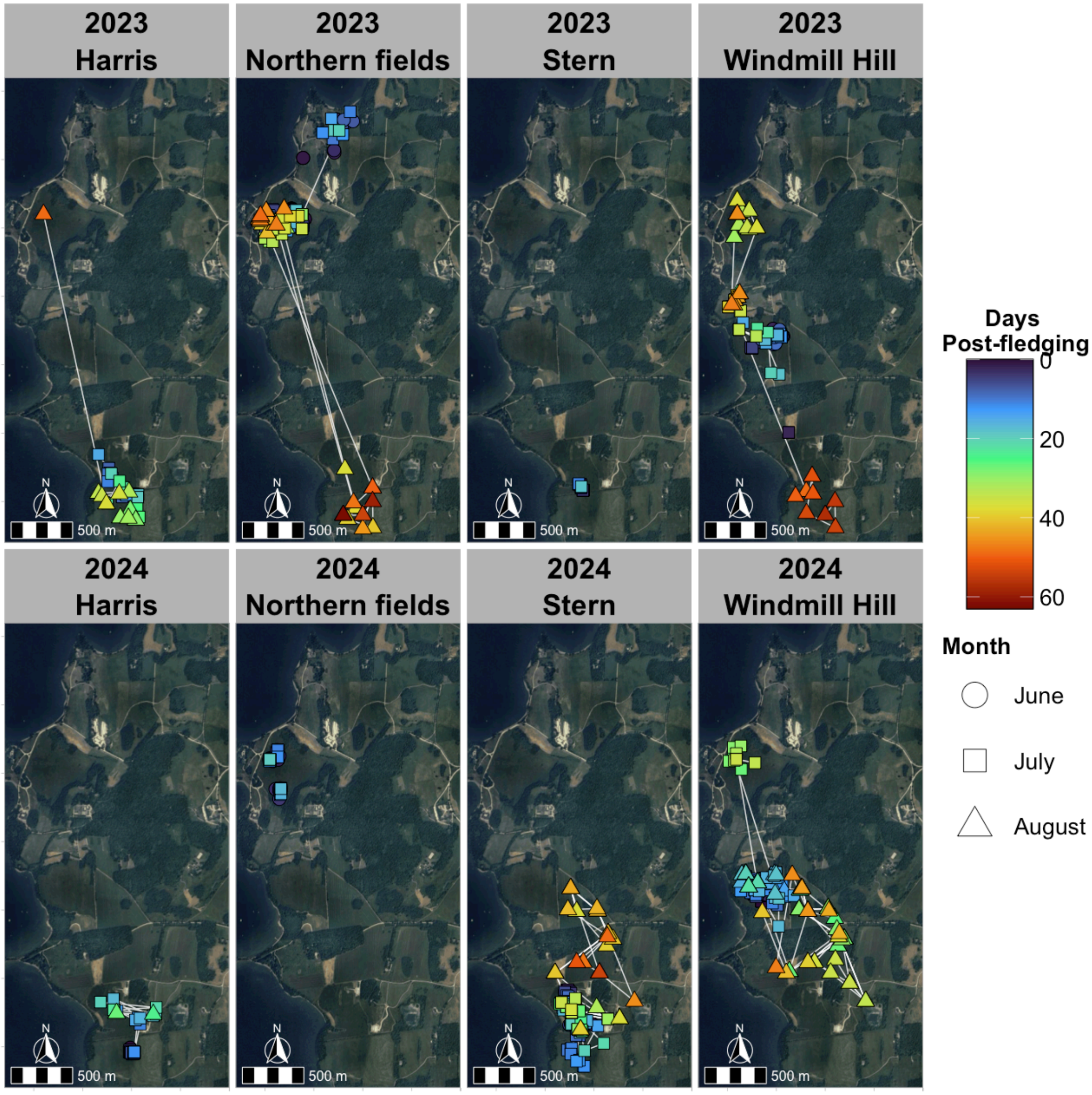

Figure 4. Telemetry tracks of 46 VHF tagged post-fledging Bobolink on Shelburne Farms, Vermont. Each frame represents all of the individuals from individual nesting field, or group of fields, separated by year. Lines connect consecutive telemetry locations and do not represent exact movement.

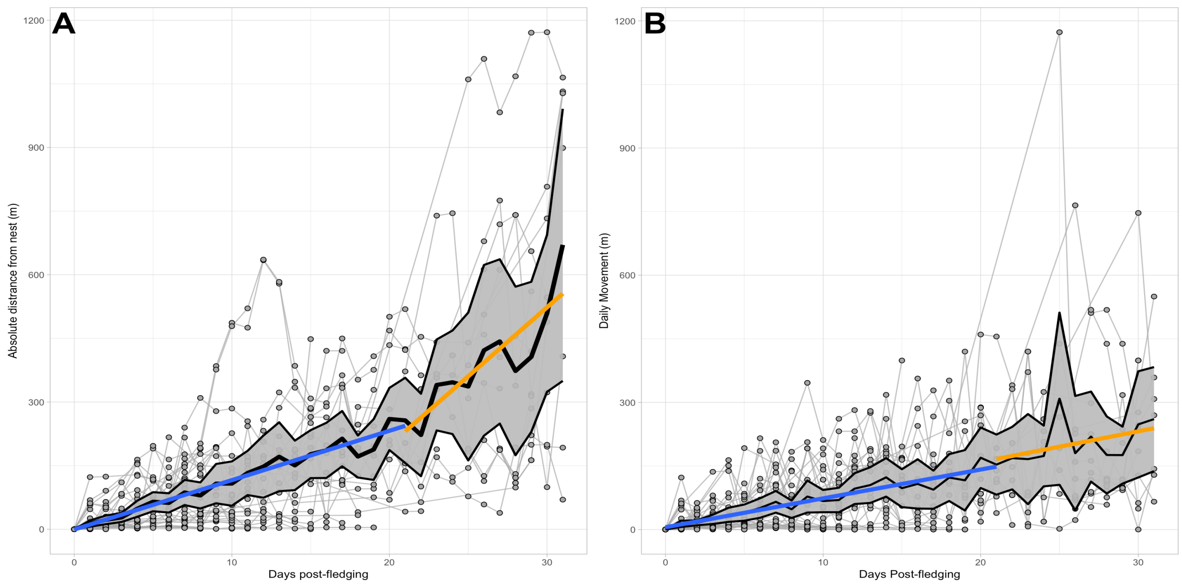

Figure 5. A: Displacement of 46 post-fledging Bobolink from their nest over the first month post-fledging. B: Distance traveled by 46 post-fledging Bobolink between subsequent daily telemetry fixes. Thin grey lines indicate individual birds, while the black line represented the average for each day and the gray polygon represents the 95% confidence interval. The blue line is the trendline from days 0 through 21 post-fledging; the orange line is the trendline from days 21 through 31 post-fledging.

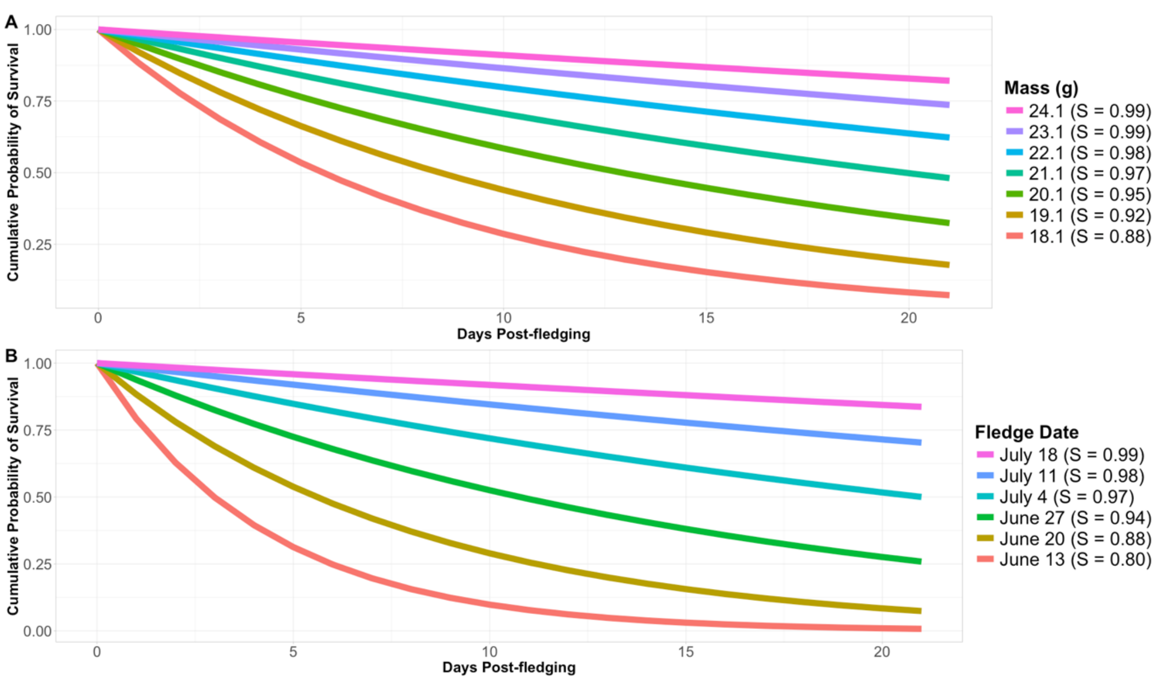

Figure 6. The modeled 21-day cumulative survival probability of VHF tagged post-fledging Bobolink as a function of A: fledge date, B: and mass at the time of tagging. Tracked birds' respective fledge date and mass at the time of tagging are represented by circles

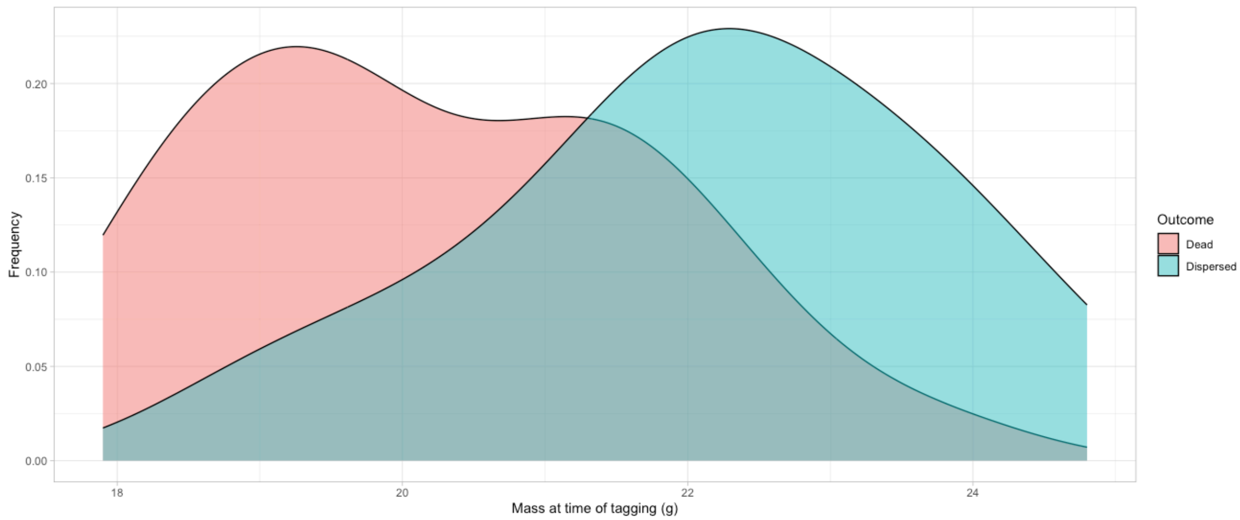

Figure 7. Frequency of mass of 44 VHF tagged post-fledging Bobolink that died during the tracking period (Dead) or successfully underwent natal dispersed (Dispersed).

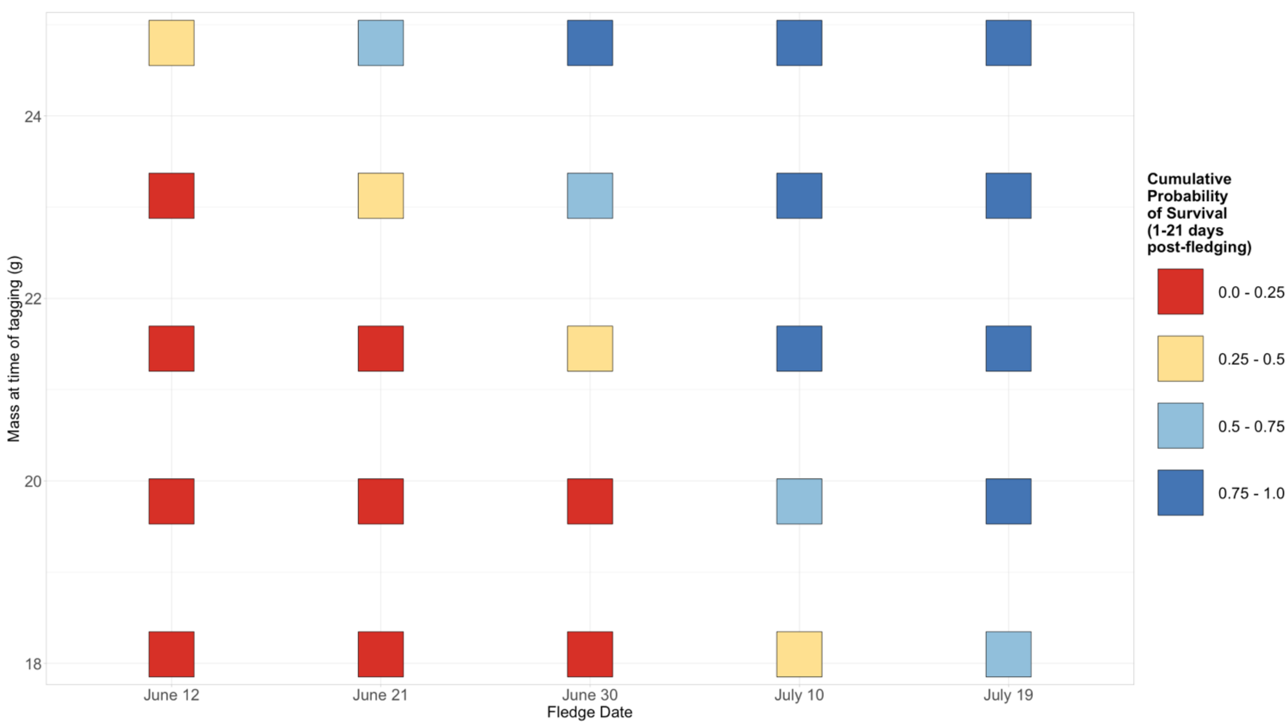

Figure 8. The modeled 21-day cumulative survival probability of 44 VHF tagged post-fledging Bobolink as a function of fledge date and mass at the time of tagging.

Table 1. Parameter estimates of initial settlement abundance of male Bobolink as a function of invasive plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.05 ± 0.23.

Variable	β	CI	SE	p(**α** - 0.05)
Invasive	< 0.01	-0.01 – 0.01	0.01	0.51
Thatch	-0.01	-0.03 – 0.1	0.01	0.34
Understory	0.23	-0.24 – 0.7	0.24	0.34

Table 2. Parameter estimates of post-settlement abundance of male Bobolink as a function of invasive plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.13 ± 0.36.

Variable	β	CI	SE	p(**α** - 0.05)
Invasive	-0.01	-0.02 – 0.01	0.01	0.38
Thatch	-0.01	-0.03 – 0.01	0.01	0.31
Understory	0.15	-0.36 – 0.66	0.26	0.57

Table 3. Parameter estimates of initial settlement abundance of female Bobolink as a function of invasive plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.06 ± 0.25.

Variable	β	CI	SE	p(**α** – 0.05)
Invasive	< 0.01	-0.1 – 0.02	0.01	0.65
Thatch	-0.02	-0.05 – 0.01	0.02	0.19
Understory	0.43	-0.31 – 1.17	0.38	0.25

Table 4. Parameter estimates of post-settlement abundance of female Bobolink as a function of invasive plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.1 ± 0.32.

Variable	β	CI	SE	p(**α** – 0.05)
Invasive	< -0.01	-0.02 – 0.02	0.01	0.95
Thatch	-0.02	-0.05 – 0.01	0.02	0.22
Understory	0.37	-0.39 – 1.13	0.39	0.34

Table 5. Parameter estimates of initial settlement abundance of male Bobolink as a function of select plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.03 ± 0.31.

Variable	β	CI	SE	p(**α** - 0.05)
Forage grasses	0.02	< -0.01 – 0.04	0.01	0.09
Reed canary grass	0.02	< 0.01 – 0.05	0.01	**0.04**
Thatch	< -0.01	-0.02 – 0.02	0.01	0.91
Smooth bedstraw	0.03	< -0.01 – 0.06	0.02	0.09
Understory	0.69	0.06 – 1.31	0.32	**0.03**

Table 6. Parameter estimates of post-settlement abundance of male Bobolink as a function of select plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.09 ± 0.23.

Variable	β	CI	SE	p(**α** - 0.05)
Forage grasses	0.02	< -0.01 – 0.05	0.01	0.08
Reed canary grass	0.02	-0.01 – 0.05	0.02	0.18
Thatch	< -0.01	-0.03 – 0.02	0.01	0.8
Smooth bedstraw	0.01	-0.03 – 0.05	0.02	0.69
Understory	0.8	-0.04 – 1.63	0.43	0.06

Table 7. Parameter estimates of initial settlement abundance of female Bobolink as a function of select plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.65 ± 0.81.

Variable	β	CI	SE	p(**α** - 0.05)
Forage grasses	0.02	-0.01 – 0.05	0.01	0.11
Reed canary grass	0.03	< 0.01 – 0.06	0.02	**< 0.05**
Thatch	-0.01	-0.04 – 0.02	0.02	0.59
Smooth bedstraw	0.03	-0.02 – 0.07	0.02	0.29
Understory	1.04	0.11 – 1.96	0.47	**0.03**

Table 8. Parameter estimates of post-settlement abundance of female Bobolink as a function of select plant species and thatch percentage. Estimates are on a log scale. Random effect variance = 0.04 ± 0.2.

Variable	β	CI	SE	p(**α** - 0.05)
Forage grasses	0.02	-0.01 – 0.05	0.01	0.13
Reed canary grass	0.03	0.01 – 0.06	0.02	**< 0.05**
Thatch	-0.01	-0.04 – 0.02	0.02	0.54

Smooth bedstraw	< 0.01	-0.05 – 0.05	0.03	0.88
Understory	1.02	0.08 – 1.97	0.48	**0.03**

Table 9. Parameter estimates of initial female Bobolink settlement abundance of all individuals using a quasi-Poisson distribution. Estimates are on a log scale. Forage grasses mean: 54.58 ± 22.2. Reed canary grass: 6.8 ± 13.67. Thatch: 11.46 ± 15.47. Smooth bedstraw: 9.4 ± 7.68.

Variable	β	CI	SE	p(**α** - 0.05)
Forage grasses (standardized)	-0.03	-0.07 – 0.01	0.02	0.15
Reed canary grass (standardized)	-0.02	-0.06 – 0.01	0.02	0.18
Thatch (standardized)	0.05	< -0.01 – 0.11	0.03	0.07
Smooth bedstraw (standardized)	-0.05	-0.1 – 0.01	0.03	0.09
Understory	-0.1	-0.21 – < 0.01	0.05	0.06

Table 10. Kaplan-Meier known-fate survivorship model selection results for VHF-tracked post-fledging Bobolink survivorship (days 1 through 31 post-fledging).

Model	AICc	ΔAICc	Weight	Deviance
S(~Nestling Mass + Fledge Date)	178.62	0.00	0.99	172.57
S(~Fledge Date)	188.67	10.05	< 0.01	184.64
S(~Nestling Mass)	189.71	11.09	< 0.01	185.69
S(~Days post-fledging)	195.03	16.41	< 0.01	191.01
S(~Intercept-only)	196.8	18.18	< 0.01	194.79
S(~Year)	197.44	18.81	< 0.01	193.41
S(~Management)	198.52	19.9	< 0.01	194.5

Table 11. Parameters from the top-fitting Kaplan-Meier known-fate survivorship model for post-fledging Bobolink survival (days 1 through 31 post-fledging).

Variable	β	SE	95% β CI	Odds Ratio
Nestling Mass	0.44	0.14	0.18 – 0.71	1.55
Fledge Date	0.1	0.03	0.04 – 0.16	1.11

Table 12. Occurrence model selection results for VHF-tracked post-fledging Bobolink.

Model	K	ΔAIC	Weight	LL
Openness + EdgeDist + Nestling Mass	8	0.00	> 0.99	-6975.11

Openness + Nestling Mass	7	55.95	0.00	-7004.09
Edge Distance + Nestling Mass	7	446.71	0.00	-7199.46
Openness + Edge Distance	7	883.58	0.00	-7417.90

Table 13. Parameters from the top-fitting generalized linear model of post-fledging Bobolink occurrence.

Variable	β	SE	95% β CI	Odds Ratio
Openness	4.00	0.33	3.36 – 4.64	54.49
Nestling Mass	0.41	0.24	-0.07 – 0.89	1.51
Edge Distance	0.28	0.04	0.21 – 0.35	1.33

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