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Diverse demographic factors influence apparent juvenile survival in a migratory songbird

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Abstract. To better understand the dynamics of avian populations and their role in population trends, we require an in-depth understanding of the factors influencing the survival of adults and juveniles. However, assessing survival in juveniles is often challenging, especially in small, migratory species where individuals typically disperse from the study area and are not available for recapture in subsequent years. Bobolinks (*Dolichonyx oryzivorus*) are a long-distance migrant that exhibits natal philopatry in at least one population, allowing for more comprehensive juvenile survival analyses than in many other long-distance avian migrants. Using a 17-yr dataset from two sites representing a Vermont population of Bobolinks, we used Program MARK to assess factors influencing apparent juvenile survival, including factors related to nesting timing, nest attempt number, the philopatric behaviors of relatives, body mass, brood size, and agricultural management scheme. Our top models indicated that nest attempt number and whether or not a nest mate also survived and returned to breed locally were important factors explaining variation in apparent survival in juvenile Bobolinks. Specifically, juveniles from first nest attempts that fledged earlier in the season, with siblings that did not survive and return to breed locally, showed higher apparent survival. Factors such as site and the philopatric behavior of females associated with nests also appeared in top-ranking models, while factors such as body mass and brood size did not. These results indicate the importance of providing high-quality breeding habitat to birds early in the season when juvenile survival is greatest and indicate that individuals may be utilizing inbreeding avoidance strategies. These results provide new insight into the ecological and agricultural management factors influencing survival in migratory species that use managed habitats and underscore the importance of integrating juvenile survival data into current management schemes to better support this and other declining species.

Key words: Bobolink; *Dolichonyx oryzivorus*; juvenile survival; nesting effort; parental care; philopatry; Vermont.

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INTRODUCTION

An understanding of the factors influencing survival of different age cohorts is essential in order to truly understand the dynamics of changing populations, requiring assessments of both adult and juvenile survival. While adults may repeatedly return to breeding sites, juveniles may not be encountered again after leaving a

nest due to dispersal, making survival analyses challenging (Maness and Anderson 2013). As a result, in avian populations much of the research on juvenile survival has only focused on the post-fledging period, the period of time between fledging and dispersal (Cox et al. 2014, Naef-Daenzer and Gruebler 2016), or has focused on non-migratory species that exhibit only small-scale dispersal (Ringsby et al. 1998, Rodriguez

et al. 2016). While these studies have investigated factors impacting the short-term survival of young birds, more research that looks at survival during the entire first year, from fledging to first reproductive attempt, is needed to better understand the impact of juvenile survival rates on population growth rates.

In many species, young birds are not re-encountered by researchers post-fledging, making an accurate estimate of apparent juvenile survival challenging; instead, many survival analyses have focused solely on this post-fledging period. Despite the challenges associated with measuring juvenile survival past the post-fledging period and through the first year, limited research has measured survival during this period, especially in residential species, where juveniles are more likely to recruit to their natal or other local breeding population (Hetmanski 2007, Medeiros and Freed 2009, Rodriguez et al. 2016, Sonnenberg et al. 2019), or larger avian species, where active tracking technologies are more feasible (Alderman et al. 2010, Afan et al. 2019, Cheng et al. 2019). Research on small, migratory species has mostly focused on populations exhibiting some degree of natal philopatry (Brown and Roth 2004, Tarof et al. 2011, Perlut and Strong 2016, Anich et al. 2017), which allows for monitoring of individuals from fledging through adulthood as individuals return to their natal sites to breed.

Across species, several factors are known to impact first-year survival of juvenile birds, including both migratory and non-migratory species. Fledging timing is one factor that influences apparent juvenile survival, albeit idiosyncratically across avian species, with earlier fledging (Tarof et al. 2011, Maness and Anderson 2013, Cheng et al. 2019), intermediate fledging (Tarwater and Brawn 2010, Rodriguez et al. 2016), and later fledging (Ringsby et al. 1998) producing higher survival, depending on species. Mass and nestling condition also influence apparent juvenile survival somewhat idiosyncratically, with greater mass (Magrath 1991, Ringsby et al. 1998, Monros et al. 2002, Greno et al. 2008, Tarwater and Brawn 2010, Maness and Anderson 2013, Rodriguez et al. 2016) producing higher survival in some species and lower mass (Perlut and Strong 2016) producing higher survival in others. However, mass showed no

influence on apparent survival in several other avian species (Brown and Roth 2004, Anich et al. 2017). Factors such as brood size (Ringsby et al. 1998, Tarof et al. 2011, Maness and Anderson 2013, Perlut and Strong 2016), sex (Tarwater and Brawn 2010, Maness and Anderson 2013, Perlut and Strong 2016, Anich et al. 2017), and study site (Perlut and Strong 2016, Anich et al. 2017) have shown little to no influence on apparent juvenile survival.

Bobolinks are long-distance migratory songbirds that exhibit relatively high rates of natal philopatry in some populations (Fajardo et al. 2009, Cava et al. 2016), allowing for analysis of factors that influence apparent juvenile survival, as individuals often return to their natal fields and are subsequently recaptured. As a polygynous grassland-obligate songbird, Bobolinks breed in grasslands and hayfields in northern North America and overwinter in central-southern South America. Long-term habitat loss on both their breeding and wintering grounds (McCracken 2005), combined with detrimental haying regimes (Perlut et al. 2006) and pesticide use (Renfrew and Saavedra 2007, Parsons et al. 2010), among other factors, has resulted in an annual population decline of 2.3% throughout their breeding range since 1966 (Sauer et al. 2019). Given these declines, much research has focused on how hayfield management impacts reproductive success (Perlut et al. 2006) and how these factors influence adult survival (Perlut et al. 2008a, Perlut and Strong 2011). In addition, an earlier investigation into juvenile survival in Bobolinks identified the interaction between mass and fledging date as an important influence, with lighter nestlings showing greater survival than heavier nestlings across the nesting season, and heavier nestlings showing greater survival the earlier they fledged in the season (Perlut and Strong 2016). Other factors, such as maternal and paternal investment, as well as their interactive effects with factors such as nestling mass and fledging date, were not included in prior analyses. Given the importance of juvenile recruitment in population dynamics, improving the conditions for juvenile survival of Bobolinks could help reduce the rate of population decline for Bobolinks (Perlut et al. 2008b) and other grassland birds that use managed habitats.

Here we offer additional insight into the factors influencing apparent juvenile survival in a polygynous population of Bobolinks that breed in hayfields in the Champlain Valley of Vermont, USA. Specifically, we sought to include adult nesting effort and offspring care, in addition to factors such as nestling mass and management scheme, in our analysis. We predicted that first nest attempts should yield greater apparent survival in comparison to subsequent attempts due to a combination of more preparation time prior to migration and higher quality eggs and parental care (Wittenberger 1978, Nager et al. 2000, Perlut and Strong 2016). Given the increased parental care provided by males to offspring of their primary, or first-mated, females compared to those of their secondary social mates (Renfrew et al. 2020), we predicted that nestlings in primary nests would have greater survival than nestlings in nests with non-primary females. For nestlings with siblings that also exhibited natal philopatry, we predicted lower apparent juvenile survival due to inbreeding avoidance strategies, as nest mates dispersed outside of the study area and were not observed as adults (Szulkin and Sheldon 2008). Similarly, we predicted that if adult males and females associated with nests were originally born locally, then their offspring may either (1) enjoy greater survival due to the application of prior experience regarding nest site quality and local resource availability or (2) have reduced apparent survival due to greater dispersal to avoid parent-offspring inbreeding (Szulkin and Sheldon 2008). If effort invested into parental care is influential in juvenile survival, then we would predict that apparent juvenile survival should decrease with increasing brood size (Styrsky et al. 2005); however, if our analyses are consistent with prior work in Bobolinks, then brood size may have no influence on survival (Perlut and Strong 2016). We predicted that lower mass would result in greater apparent juvenile survival, possibly due to increased site fidelity as young birds spend additional time foraging locally, as indicated in previous research on Bobolinks (Perlut and Strong 2016). In accordance with research on reproductive success (Perlut et al. 2011) and population dynamics in Bobolinks (Perlut et al. 2008b) in agricultural settings, we predicted that late-season mowing of hayfields would result in greater apparent

juvenile survival than other management schemes, although previous research has indicated that management may not be as important in explaining variation in survival as other factors (Perlut and Strong 2016).

METHODS

Study area

We utilized Bobolink data collected from 2002 to 2018 within the Champlain Valley in hayfields located in Shelburne, Chittenden County, Vermont (44°23'31.4" N, 73°16'23.1" W). The Champlain Valley has 146,000 ha of managed grasslands located within a mosaic of agricultural land, forests, and increasing human development (NASS 2012). Our study monitored Bobolinks in two hayfields: (1) a late-hayed field, mowed annually in August or September and (2) an early-hayed field, mowed once between mid-May and early June and a second time 34–52 d (2002–2007) or a minimum of 65 d (2008–2018) after the initial mow. In this study area, reproductive success and adult apparent survival is highest in late-hayed fields (Perlut et al. 2008); however, shifting the timing of the second harvest on early-hayed field in 2008–2018 from ~35 to 65 d after the first harvest notably increased reproductive success to a level nearly equal to that of the late-hayed field (Perlut et al. 2011).

Field methods

On each study site, we collected breeding data for Bobolinks during each breeding season (late-May to late-July). Adults at each site were caught using mist nets and given a combination of a metal US Geological Survey (USGS) band and three plastic color bands that allowed for individual identification. We collected morphological measurements from each adult bird. We located nests through a combination of flushing females off of nests and behavioral observations. Once found, each nest was monitored every 1–2 d to track the fate of the nest and to determine the social parents. In addition, we banded and weighed all nestlings. For polygynous males, earlier-formed social pairings were considered higher ranked (i.e., primary) compared to later-formed social pairings (i.e., secondary, tertiary).

Each year, we conducted surveys to locate birds that returned to their natal region,

beginning with surveys on our six primary study fields, each ranging from 16 to 20 ha. In addition, between 2005 and 2013 we searched fields within 1.5 km of our study sites, between 2014 and 2017 we searched fields within 10 km, and in 2018 we searched fields within 20 km of our study sites. These additional fields ranged in size from 1 to 41 ha and were searched twice annually by groups of two to ten individuals (Fajardo et al. 2009, Cava et al. 2016). Banded birds were caught using 12 m mist nets. We identified returning fledglings by their single metal band; these birds received a unique combination of three color bands upon recapture.

Study sample

For our survival analyses, we selected only nests with at least one natal philopatric young ($n = 97$) and included all nestlings from these nests ($n = 400$). In total, we included 68 nests from EM and 29 from WH.

Survival analyses

We ran time-dependent multi-state models with an unknown state (Hidden Markov Model, HMM; Conn and Cooch 2009) in Program MARK version 9.0 (White and Burnham 1999; *personal communication* with EG Cooch and WL Kendall 2019) to assess apparent juvenile survival; we ranked individual models based on their Akaike's Information Criterion (AIC) values, a method that accounts for both the number of parameters in the model and any associated error variance. We considered all models with $\Delta\text{AICc} \leq 2$ relative to the top model biologically significant in explaining variation in apparent juvenile survival (Burnham and Anderson 2002). We model-averaged any effect that appeared in more than one model with a $\Delta\text{AICc} \leq 2$ (Burnham and Anderson 2002). We compiled encounter histories using an assigned (male, female) or unknown (unknown sex) state relative to sex and analyzed these histories as a function of ten individual covariates (Table 1), including two-way interactive effects, and two- and three-factor additive effects (see Appendix S1 for full model set). We converted continuous covariates to standardized Z-scores (range = 0 to 1) before inclusion in survival analyses; binary covariates were not converted. The probability of detection was grouped into four approaches based on the

distance searched: (1) 2002–2004, searches only conducted on primary study fields; (2) 2005–2013, searches conducted on fields within 1.5 km of primary study fields; (3) 2014–2017, searches conducted on fields within 10 km of primary study fields; and (4) 2018, searches conducted on fields within 20 km of primary study fields.

RESULTS

Of the 400 nestlings sampled between 2002 and 2018, we relocated 124 (31%) that survived and returned to breed on or near their natal fields (≤ 3 km) as adults. We identified six models with $\Delta\text{AICc} \leq 2$ that explained variation in apparent juvenile survival in Bobolinks (Table 2).

The top two models (combined AICc weight = 0.38189, representing the combined weighted likelihood of the models) included the additive and interactive effects of (1) maternal nest number, a standardized value relating to the maternal nest attempt number (i.e., first, second, third, etc. of the total number of attempts) (Fig. 1), and (2) nest sibling return, whether or not a nest mate also survived and returned to breed on local fields (Fig. 2; Table 2); these two factors appeared in all six models with similar trends observed in both males and females. Nestlings born to mothers breeding earlier in the season, especially those mothers attempting their first of two or more broods ($n = 4$ nests; average fledge date = June 20th), had higher apparent survival (0.70 (0.31–0.92 95% CI) female; 0.86 (0.69–0.94) male) than nestlings born to mothers that only nested once in a season ($n = 83$ nests; average fledge date = June 29) or those attempting second (0.58 (0.24–0.81 95% CI) female; 0.81 (0.63–0.89) male; $n = 8$ nests; average fledge date = July 8) or third broods (0.46 (0.19–0.68 95% CI) female; 0.75 (0.56–0.85) male; $n = 1$ nest; average fledge date = July 21; Fig. 1). In addition, apparent survival was lower (0.37 (0.17–0.64) female; 0.71 (0.53–0.82) male) for nestlings whose siblings survived and returned to their natal field ($n = 328$) than for nestlings with no siblings that survived and returned (0.82 (0.42–0.95) female, 0.90 (0.77–0.94) male; $n = 72$; Fig. 2).

In the top ranked model, average apparent survival across years was 0.60 (95% CI: 0.19–0.78),

Table 1. All covariates included in juvenile survival analyses in Bobolinks (*Dolichonyx oryzivorus*) in Program MARK.

Name	Meaning	References
Brood size†	Number of siblings in a nest	Naef-Daenzer and Gruebler (2016); Perlut and Strong (2016)
Mass†	Mass of each nestling standardized by the age of the bird when it was weighed	Naef-Daenzer and Gruebler (2016); Perlut and Strong (2016)
Maternal nest number†	The social mother's nest attempt number standardized by the total number of nests she attempted in a season (lower values represent first clutches occurring earlier in the season, while higher values represent re-nests occurring later in the season)	Wittenberger et al. (1978); Perlut and Strong (2016)
Maternal philopatry	If the social mother was born and returned to breed locally (1) or not (0)	Szulkin and Sheldon (2008)
Maternal rank†	The hierarchical partnership of the social father's mate (primary female vs. secondary female, etc.) standardized by the total number of the social father's social partnerships	Renfrew et al. (2020)
Nest sibling return	Whether or not nest mates survived (1) or not (0)	Szulkin and Sheldon (2008)
Other sibling return	Whether or not siblings from the social mother's other fledged nests, outside of the natal nest of the nestling, survived (1) or not (0)	Szulkin and Sheldon (2008)
Paternal nest number†	The social father's nest attempt number standardized by the total number of nests he attempted in a season (lower values represent first clutches occurring earlier in the season, while higher values represent re-nests occurring later in the season)	Wittenberger et al. (1978); Perlut and Strong (2016)
Paternal philopatry	If the social father was born and returned to breed locally (1) or not (0)	Szulkin and Sheldon (2008)
Site	If a nestling was born on Elm Marsh (late-mowed; 1) or Windmill Hill (early mowed; 0)	Perlut et al. (2008b); Perlut et al. (2011); Perlut and Strong (2016)

† All non-binary factors were scaled using z-scores before incorporation into survival analyses.

Table 2. Top models ($\Delta AICc \leq 2$) explaining variation in apparent survival in juvenile Bobolinks (*Dolichonyx oryzivorus*).

Model	AICc	$\Delta AICc$	AICc ω_i	No. par
1. Maternal Nest Number + Nest Sibling Return	1023.869	0.000	0.190	53
2. Maternal Nest Number \times Nest Sibling Return	1023.872	0.003	0.190	52
3. Maternal Nest Number + Nest Sibling Return + Site	1024.625	0.756	0.130	55
4. Maternal Nest Number + Maternal Rank + Nest Sibling Return	1025.300	1.431	0.093	54
5. Maternal Nest Number + Maternal Philopatry + Nest Sibling Return	1025.850	1.981	0.071	54
6. Maternal Nest Number + Nest Sibling Return + Paternal Nest Number	1025.872	2.003	0.070	54

Notes: Models included either additive (+) or interactive (*) effects and included both juvenile males and females.

AICc: The adjusted/corrected Akaike Information Criteria.

$\Delta AICc$: The difference between the given model and the top model's AICc values.

AICc ω_i : The weight associated with a given model; the amount of variation in apparent survival explained by a given model (value out of 1).

No. Par.: The number of estimated probabilities (parameters) included in a given model.

Covariate explanations can be found in Table 1.

varying from 0.03 to 1, with males showing greater apparent survival (0.76 (95% CI: 0.22–0.86)) than females (0.45 (95% CI: 0.16–0.70)). In addition, the average detection probability for first-year birds in this model was 0.48 (95% CI: 0.16–0.70) in 2002–2004, 0.51 (0.26–0.72) in 2005–2013, 0.51 (0.14–0.77) in 2014–2017, and 0.60 (0.34–0.78) in 2018.

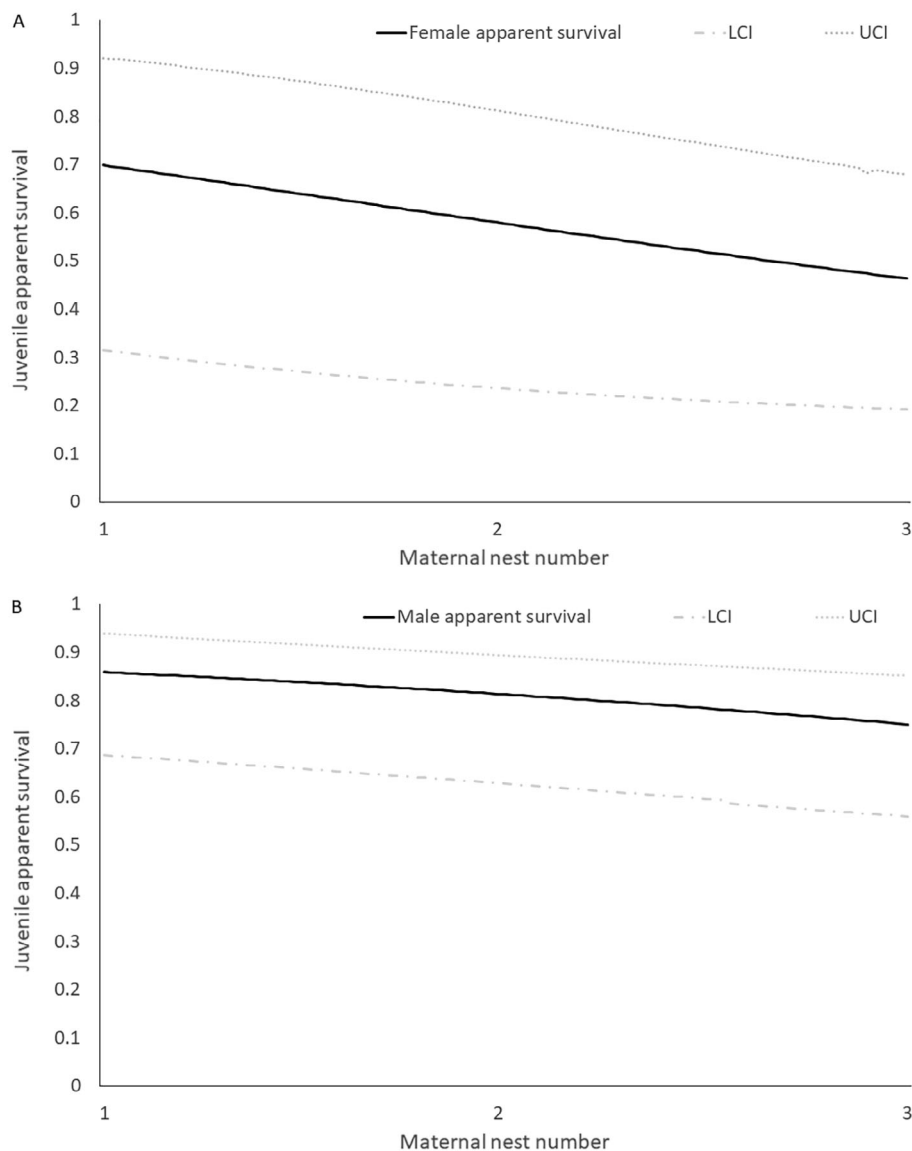


Fig. 1. Apparent survival of juvenile Bobolinks (*Dolichonyx oryzivorus*) decreased with increasing maternal nest number for both females (A) and males (B). On average, first nest attempts fledged ~23 June ($n = 87$), second attempts fledged ~8 July ($n = 8$), and a single third attempt fledged on 21 July.

In addition to maternal nest number and nest sibling return, which continued to explain variation in the third-ranked model, site also helped explain variation in apparent survival. Nestlings born on the early-hayed field showed slightly higher apparent survival (0.65 (95% CI: 0.32–0.85)) than those born on the late-hayed field (0.55 (95% CI: 0.32–0.85)). In the fourth-ranked model, maternal rank, or whether or not a nest

was associated with a polygynous male's primary female, secondary female, etc., helped explain variation in addition to maternal nest number and nest sibling return. Among the nestlings of polygynous males, nestlings in primary nests ($n = 22$ nests; average fledge date = June 27th) had higher survival than those from secondary ($n = 12$ nests; average fledge date = July 4th) or tertiary nests ($n = 3$ nests; average fledge

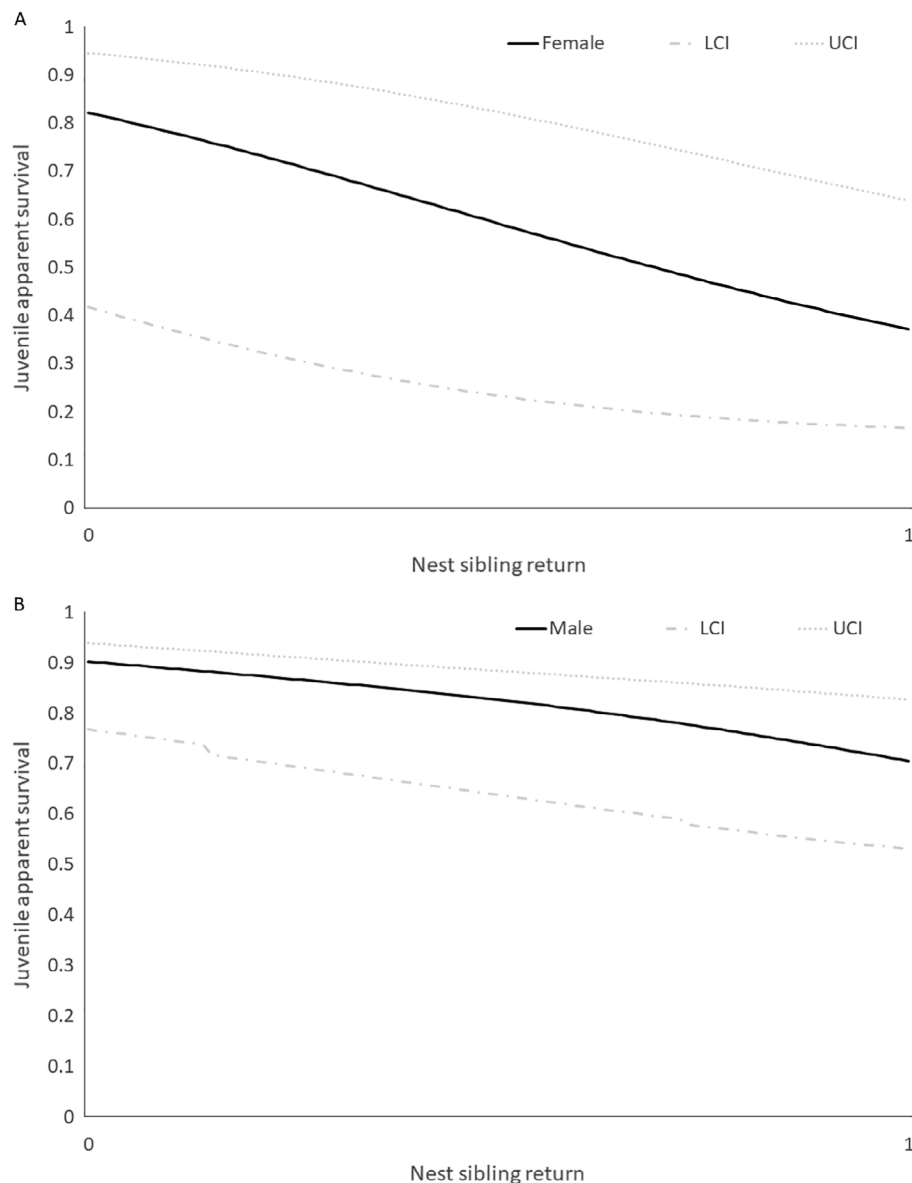


Fig. 2. The impact of surviving nest mates on juvenile apparent survival of Bobolinks (*Dolichonyx oryzivorus*) nesting in agricultural grasslands of the Champlain Valley of Vermont. Nestlings were categorized as either having nest mates that returned locally (1) or not having returned locally (0).

date = July 9th). In addition to maternal nest number and nest sibling return, whether or not a mother was born locally helped explain variation in survival in the fifth-ranked model. Nestlings with mothers that were born on local fields showed slightly greater survival (0.63 (95% CI: 0.38–0.81)) than nestlings whose mothers were not born locally (0.60 (95% CI: 0.38–0.78)). In the

sixth-highest ranking model, paternal nest number joined maternal nest number and nest sibling return in explaining variation in survival. Nestlings born to social fathers breeding earlier in the season, especially those attempting their first of two or more broods ($n = 24$; average fledge date = June 25th), had higher survival than nestlings born to social fathers that only nested once

in a season ($n = 40$ nests; average fledge date = June 28th) or those attempting second ($n = 13$ nests; average fledge date = July 4th), third ($n = 3$ nests; average fledge date = July 9th), or fourth broods ($n = 1$ nest; fledge date = July 5th).

Other factors investigated, such as brood size, nestling mass, the number of surviving siblings from a mother's prior nest attempts, and whether or not the social father was originally born locally did not explain variation in survival in our analyses.

DISCUSSION

Of the ten covariates included in our models, maternal nest number and nest sibling return were the two most important sources of variation in apparent survival of juvenile Bobolinks, with four additional covariates—site, maternal rank, maternal philopatry, and paternal nest number—explaining variation in some models. In addition, juvenile males showed higher overall apparent survival than females. Covariates such as brood size, paternal philopatry, mass, and other sibling return did not help to explain variation in apparent juvenile survival.

Top covariates: Maternal nest number, and nest sibling return

Maternal nest number, a standardized value relating to the maternal nest attempt number (i.e., first, second, third of the total number of attempts), and nest sibling return, whether or not a nest mate survived and returned to breed on local fields, were the two covariates present in all top models.

As females attempted second and third broods, apparent juvenile survival decreased with each nest attempt. In Bobolinks, females typically lay fewer eggs with each subsequent nest attempt, potentially due to the energy expenditure associated with prior nest attempts (Perlut et al. 2006, Renfrew et al. 2020). In Lesser Black-backed Gulls (*Larus fuscus*), earlier laid eggs were of higher quality than subsequently laid eggs and were more likely to successfully fledge a chick (Nager et al. 2000). If a similar pattern exists in Bobolinks and as females attempt second clutches the quality of their eggs may decline, then this may ultimately result in reduced survival of offspring.

Single clutches are common with Bobolinks and re-nesting behavior is rare; for example, in a New York population, single attempts comprised 93.7% of all nest attempts in a given season (Gavin 1984). Similarly, in our sample single nest attempts represented 88% of the total nests included in analyses.

Alternatively, this trend in decreasing apparent survival with increasing nest attempt may be associated with fledging date, as secondary nest attempts that may have included lower quality eggs would have also occurred later in the breeding season. Fledging date was important in an earlier analysis that investigated apparent survival in juvenile Bobolinks; however, while Perlut and Strong's (2016) analysis indicated an interaction of fledging date with nestling mass, mass did not explain variation in survival in our models using an additional six years of data (Appendix S1). Greater survival with earlier fledging has also been noted in other migratory species, such as the Purple Martin (*Progne subis*, Tarof et al. 2011), and White Stork (Cheng et al. 2019), while other species show greater survival with intermediate or late fledging, although many of these species are non-migratory (House Sparrow, Ringsby et al. 1998; Western Slaty-Antshrike, Tarwater and Brawn 2010; Great Tit, Rodriguez et al. 2016).

For long-distance migrants, an earlier fledge date may allow for more time to learn and practice independent foraging techniques, as well as more time to build up fat stores prior to migration. Post-fledging, Bobolinks take up to ~ 16 d to make sustained flights and continue to make contact calls with adults for ~ 20 d post-fledging; however, little is known about the timing to full independence (Renfrew et al. 2020). In post-fledging survival analyses, timing since fledging was an important factor, likely due to the steep learning curve associated with learning to independently forage for food after leaving the nest (Naef-Daenzer and Gruebler 2016). For long-distance migrants that survive this initial challenge post-fledging and learn to forage independently, they now have the duration of the breeding season to practice these strategies and acquire food. Thus, timing of nest attempts may be influencing the survival results seen here.

In addition to maternal nest number, nest sibling return was important in explaining variation

in apparent juvenile survival. Survival of nestlings was greater when no nest mates exhibited natal philopatry. This result corresponds with our previous work, where a suite of ecological and demographic factors, including the presence of an opposite-sex parent or sibling on the natal field, was unable to explain variation in natal dispersal distance (Cava et al. 2016). As close relatives survived and returned to breed on their natal field, the likelihood of encountering and subsequently breeding with relatives would be high given the high rates of natal philopatry in our study population (Fajardo et al. 2009, Cava et al. 2016); thus, low apparent survival may result from individuals dispersing to non-natal breeding grounds (>20 km away) as a mechanism for avoiding inbreeding, thus eliminating those individuals from the sampled population (Szulkin and Sheldon 2008). Such inbreeding avoidance strategies can be seen in European Storm Petrels (*Hydrobates pelagicus*, Bonadonna and Sanz-Aguilar 2012) and Long-tailed Tits (*Aegithalos caudatus*, Sharp et al. 2005) which are both able to recognize relatives and avoid mating with them. Savannah Sparrows (*Passerculus sandwichensis*) also show evidence of inbreeding avoidance through separation of relatives within breeding fields in populations with similarly high natal philopatry rates (Wheelwright and Mauck 1998) or through reduced rates of natal philopatry (Cava et al. 2016). Taken together, we do not know yet know the mechanism by which an individual Bobolink would know whether or not to disperse.

This pattern of reduced survival of individuals when nest mates survive and return to breed locally could also indicate a skewed allocation of parental care by adult Bobolinks. In nests with multiple nestlings, it is possible that Bobolink parents may focus their time, energy, and resources on only a few of their nestlings to increase the likelihood of survival of some offspring, resulting in reduced survival of others. This behavior has been observed in Shoebills (*Balaeniceps rex*), where females lay two eggs, but only one chick typically fledges due to the unequal allocation of parental care (Mullers and Amar 2015). Alternatively, nestlings that hatch first and are of higher quality may be able to better compete with their nest mates for food, resulting in variation in condition among nest mates

(Ostreiher 1997). In Tree Swallows (*Tachycineta bicolor*), adults fed nestlings based on nestling-controlled signals such as begging order and proximity to nest edge (Whittingham et al. 2003). Such factors could result in several young within a nest showing high survival while others exhibit low survival, as identified in this population. However, a previous analysis indicated that lighter nestlings had greater survival than heavier ones (Perlut and Strong 2016); if this trend is representative of factors impacting survival in this species, then skewed parental care is an unlikely explanation for the pattern of survival we observed.

Additional influential covariates: site, maternal rank, maternal philopatry, paternal nest number, and sex

While not present in all top models, the covariates site, maternal rank, maternal philopatry, and paternal nest number each explained some variation in apparent juvenile survival in our population.

Site

We investigated apparent juvenile survival of Bobolinks on two fields: (1) a hayfield mowed annually each August or September, and (2) a hayfield mowed twice annually, once between mid-May and early June and a second time 34–52 d (2002–2007) or a minimum of 65 d (2008–2018) after the initial mow. Young birds born on the early-hayed field showed greater survival (0.65) than those born on the late-hayed field (0.55), although prior to the change of management and mowing regimes on the early-hayed field in 2008, no Bobolinks born on the field survived and returned to breed on local fields. These survival estimates between fields are consistent with research indicating that reproductive success in Bobolinks is greater on fields managed using bird-friendly practices, such as those employed on the early-hayed field since 2008 (Perlut et al. 2011); however, a previous analysis of apparent juvenile survival indicated no difference between sites (Perlut and Strong 2016). Our results may indicate the importance of long-term implementation of management schemes that balance bird and farmer needs. Alternatively, these results could indicate the importance of ecological differences between the fields, such as

vegetation composition, microclimates, or insect diversity and availability, which may be influencing differences in apparent juvenile survival between the two sites, and may be changing over time.

Maternal rank

Young birds born in the secondary and tertiary nests of polygynous males had lower apparent juvenile survival than young born in primary nests. Across Bobolink populations, males typically assist in feeding nestlings associated with their primary females, but feed nestlings less, or not at all, in nests associated with their non-primary females (Renfrew et al. 2020). In our population specifically, feeding is typically female-dominated, with males representing 28% of feeding visits made by adults to nests (Little et al. 2009). Thus, for nestlings in nests of secondary or tertiary females, they may only receive food from one, rather than two parents, both while in the nest and immediately after fledging when young are still dependent on their parents for food, which may negatively impact their likelihood of survival (Wittenberger 1978).

Maternal philopatry

The philopatry of the female associated with the nest (mother) helped explain variation in apparent survival of juveniles. Juvenile males and females showed higher survival when their mother was born locally, and showed reduced survival when their mother was born outside of the study site. Potentially, locally born females could provide offspring with insider knowledge regarding high-quality foraging locations that could result in greater survival or may have beneficial knowledge regarding optimal nesting locations that ultimately lead to increased offspring survival.

Paternal nest number

As paternal nest number increased, apparent juvenile survival decreased, similar to the trends noted above regarding maternal nest number. If attentiveness of males at nests decreases with increasing nest attempt, regardless of whether they are in monogamous or polygynous pairings, then it is not surprising that this trend would be similar to that of maternal rank.

Sex

Across models, juvenile males showed greater apparent survival than juvenile females. While this trend is consistent with that found in the Nazca Booby (Maness and Anderson 2013) and Swainson's Warbler (*Limnothlypis swainsonii*, Anich et al. 2017), where young males also showed greater survival than females, this trend may instead be a byproduct of a system where female-biased dispersal is occurring, as seen in natal dispersal in Bobolinks (Cava et al. 2016). Female-biased dispersal may be obscuring true survival estimates for females. Interestingly, this pattern was not observed in adult Bobolinks, where both sexes showed similar patterns of breeding dispersal (Fajardo et al. 2009). In addition, earlier survival models for adult Bobolinks indicated that males had higher survival than females (Perlut et al. 2008a), although these results differ from those previously found in juvenile Bobolinks, where survival did not differ between sexes (Perlut and Strong 2016). Similar to Bobolinks, in many avian species female-biased dispersal is the norm, resulting in an increased presence of males on natal grounds (Liberg and von Schantz 1985, Perrin and Mazalov 2000); more research is needed to better understand the different dispersal strategies utilized by the different sexes in Bobolinks and how these dispersal techniques influence apparent survival estimates.

Non-influential covariates: brood size, paternal philopatry, mass, and other sibling return

Of the covariates included in our analyses, brood size, paternal philopatry, mass, and other sibling return did not help explain variation in apparent juvenile survival. If brood size is indicative of declining allocation of parental care among nestlings, then increasing brood size should result in reduced survival of juveniles (Styrsky et al. 2005). Similarly, greater nestling mass (indicating more attentive parents and/or greater consumption of food while in the nest) should result in increased survival of juveniles (Magrath 1991, Ringsby et al. 1998, Monros et al. 2002, Greno et al. 2008, Tarwater and Brawn 2010, Maness and Anderson 2013, Rodriguez et al. 2016). However, in many species, including Bobolinks, brood size shows little to no influence on juvenile survival (Ringsby et al. 1998, Maness

and Anderson 2013, Perlut and Strong 2016), and a previous analysis indicated that a reduced mass combined with earlier fledging resulted in higher apparent juvenile survival in Bobolinks (Perlut and Strong 2016). These studies may indicate that brood size and nestling mass do not adequately represent differential parental care; the analysis of factors such as fledgling mass may be more informative regarding long-term survival trends of juveniles (Perrig et al. 2017).

Paternal philopatry, whether or not a social father was born locally, and other sibling return, whether or not a maternal sibling from a non-natal nest also survived and returned to breed locally, also did not explain variation in apparent juvenile survival. Given the reduced offspring care provided by males, social fathers do not interact with nestlings as frequently as females do, and thus may not be as important as communicators of local resource availability and quality (Wittenberger 1978, Little et al. 2009). The lack of influence of other sibling return on apparent juvenile survival may be indicative of nest-specific factors influencing survival of offspring; climatic conditions, food availability, and other such factors may impact the survival of offspring in one nest independently of those in another. In addition, identifying cues among nest mates may result in nest-specific influences on natal philopatric behavior.

CONCLUSION

In our analysis, apparent juvenile survival was highest for nestlings born to first nest attempts and whose siblings did not survive and return. These results point toward re-nesting behavior and parental care allocation, and indirectly toward fledging timing, as important influencers of apparent juvenile survival; in addition, it raises the question of the importance of inbreeding strategies and the acquisition of local knowledge as influencers of apparent survival and dispersal behaviors in juvenile Bobolinks.

We acknowledge that our results describe apparent survival estimates and not true survival, and that diverse analytical methods can be used to approach true survival (Gilroy et al. 2012, Redmond and Murphy 2012, Ergon and Gardner 2014). Moreover, our decision to not include all nests from our study fields likely

upwardly biased our apparent survival estimates (e.g., we excluded nests that fledged and none of the surviving offspring returned locally or were detected). We excluded these nests because (1) we previously analyzed first-year apparent survival values with all nests rather than a subset of nests (Perlut and Strong 2016), and (2) here we focused more on variation among surviving individuals and their non-surviving/returning siblings. Our goal was to gain further resolution to the results described in Perlut and Strong (2016).

While several of these factors are associated with the behavioral ecology of Bobolinks, such as the importance of social male investment into parental care and the time needed for young birds to prepare themselves for migration, other factors influencing apparent juvenile survival, such as the influence of fledge date and site, are potentially impacted by management of breeding landscapes. As we continue to investigate factors influencing survival in this system, it will be important to distinguish ecological and management-based factors as we consider the future management of this declining species.

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DATA AVAILABILITY

Data are available from Dryad: <https://doi.org/10.5061/dryad.80gb5mkrf>.

SUPPORTING INFORMATION

Additional Supporting Information may be found online at: <http://onlinelibrary.wiley.com/doi/10.1002/ecs2.3761/full>