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RESEARCH ARTICLE

Winter diet of Bobolink, a long-distance migratory grassland bird, inferred from feather isotopes

Rosalind B. Renfrew,[1]* Jason M. Hill,[1] Daniel H. Kim,[2] Christopher Romanek,[3] and Noah G. Perlut[4]

[1] Vermont Center for Ecostudies, Norwich, Vermont, USA
[2] Portland State University, Portland, Oregon, USA
[3] Furman University, Greenville, South Carolina, USA
[4] University of New England, Biddeford, Maine, USA
* Corresponding author: rrenfrew@vtecostudies.org

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ABSTRACT

Effective conservation of migratory bird populations depends on advancements in our understanding of processes throughout the life cycle. Fundamental information about wintering ecology (e.g., habitat use and diet composition) remains limited, which limits assessment of threats to populations during winter. Bobolink (*Dolichonyx oryzivorus*) is a year-round grassland obligate and Nearctic-Neotropical migrant that undergoes 2 complete molts each year, including a complete prealternate molt on the South American wintering grounds. This unusual winter molt provides a rare opportunity to examine, using stable isotope analysis, the timing and contribution of foraging resources in the Bobolink diet prior to northbound migration from disparate breeding populations. We compared winter diet composition among 3 breeding populations of Bobolinks and during 3 stages of winter molt using stable carbon isotope ratios. We used mixing models to compare the ratio of carbon-12 to carbon-13 isotope ($\delta^{13}C$ value) in feathers—grown on the wintering grounds but collected from individuals ($n = 105$) breeding in Vermont, Nebraska, and North Dakota, USA—to estimate diet during early, middle, and late winter molt. Across the 3 breeding populations, Bobolinks relied on C_3 sources for nearly one-third of their diet during the winter molt. Isotope data from feathers collected while growing on the wintering grounds from birds in rice vs. non-rice regions supported our assumption that C_3 signatures are primarily due to a rice diet. The proportion of rice consumed was highest during late molt, corresponding with a period of greater rice availability to Bobolinks. Our results demonstrate that rice was a substantial component of the diet throughout the winter molt and was most exploited prior to northbound migration. Research is needed on the potential trade-offs of feeding on abundant cultivated rice, including its nutritional value and associated risks and conflicts from foraging in an agricultural setting.

Keywords: Bobolink, diet, *Dolichonyx oryzivorus*, mixing model, *Oryza sativa*, prealternate molt, rice, stable carbon isotope, wintering ecology

Dieta de invierno inferida a partir de isótopos de las plumas de *Dolichonyx oryzivorus*, un ave de pastizal migratoria de larga distancia

RESUMEN

La conservación efectiva de las poblaciones de aves migratorias depende de los avances de nuestro entendimiento sobre los procesos a lo largo del ciclo de vida. Aún se cuenta con poca información fundamental sobre aspectos de la ecología de invierno, como el uso del hábitat y la composición de la dieta, lo que limita la evaluación de las amenazas a las poblaciones durante el invierno. *Dolichonyx oryzivorus* es una ave de uso obligatorio de pastizal durante todo el año y un migrante neártico-neotropical que experimenta dos mudas completas cada año, incluyendo una muda pre-alternativa completa durante la migración en los territorios de invernada en América del Sur. Esta muda inusual de invierno brinda una rara oportunidad para examinar la sincronización temporal y la contribución de los recursos de forrajeo en la dieta de *D. oryzivorus* antes de la migración hacia el norte desde poblaciones migratorias dispares usando análisis de isótopos estables. Comparamos la composición de la dieta de invierno entre tres poblaciones reproductivas de *D. oryzivorus* y durante tres estadios de la muda de invierno usando cocientes de isótopos estables de carbono. Usamos modelos mixtos para comparar el cociente de isótopos de carbono-12 con carbono-13 (valor δ13C) en plumas que crecieron en los sitios de invernada, pero que fueron colectadas de individuos ($n = 105$) que criaban en Vermont, Nebraska y Dakota del Norte para estimar la dieta a principios, mediados y fines de la muda de invierno. En las tres poblaciones reproductivas, *D. oryzivorus* confió en fuentes de C3 para cerca de un tercio de su dieta durante la muda de invierno. Los datos de isótopos de las plumas colectadas de aves que crecían en sitios de invernada en regiones arroceras versus no arroceras apoyaron nuestra suposición que las firmas de C3 se deben principalmente a una dieta de arroz. La proporción de arroz consumido fue máxima durante la muda tardía, correspondiendo con un

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período de gran disponibilidad de arroz para *D. oryzivorus*. Nuestros resultados demuestran que el arroz fue un componente sustancial de la dieta a lo largo de la muda de invierno, aprovechado mayormente antes de la migración hacia el norte. Se requieren investigaciones sobre los potenciales compromisos entre alimentarse de cultivos de arroz abundantes, incluyendo su valor nutricional, y los riesgos asociados y los conflictos a partir de forrajear en un medio agrícola.

Palabras clave: arroz, dieta, *Dolichonyx oryzivorus*, ecología de invierno, isótopo estable de carbono, modelo mixto, muda pre-alternativa, *Oryza sativa*

INTRODUCTION

An effective conservation strategy for any species requires a comprehensive understanding of how its populations are regulated via productivity and survival. In birds, breeding performance (e.g., fecundity or mass at fledging) and survival are strongly influenced by nest predators and by the quality and quantity of food consumed during the breeding season (Martin 1987, Derbyshire et al. 2015). However, influences outside of the breeding season are known to contribute to negative population trends in long-distance migrants (Hewson and Noble 2009), including grassland bird species such as Dickcissel (*Spiza americana*; Basili and Temple 1999). Nonbreeding survival can drive the population growth rate of Bobolink (*Dolichonyx oryzivorus*; Fletcher et al. 2006). Similarly, Vesper Sparrow (*Pooecetes gramineus*) survival was lower in wintering habitat with lower grass and shrub heights, potentially contributing to population declines (Macías-Duarte and Panjabi 2013). Researchers have increasingly focused on understanding how populations are influenced by processes occurring outside of the breeding season (Latta and Faaborg 2002, Marra et al. 2015, Rushing et al. 2016, Stutchbury et al. 2016), including how nonbreeding dietary and habitat choices may affect future breeding performance (Webster et al. 2002, Gurney et al. 2014).

Globally, agriculture has replaced the majority of historical grassland habitat (Hannah et al. 1995). Management and conservation efforts to stabilize grassland bird population declines have primarily focused on life history traits, habitat use, and threats influencing breeding populations, but processes influencing nonbreeding populations remain poorly understood (Vickery et al. 1999, Brennan and Kuvlesky 2005). However, known threats on the wintering grounds include mortality from incidental and deliberate exposure to insecticides (Gard and Hooper 1995, Basili 1997, Parsons et al. 2010), lethal control by humans (Renfrew and Saavedra 2007), and food shortages (Peach et al. 2001, Newton 2004). An understanding of winter habitat use, diet, and body condition is required to document the relative importance of threats and to inform agricultural management practices.

Body condition is a strong predictor of migratory behavior in passerines (Fusani et al. 2009), and poor body condition, including inadequate premigratory fat reserves, may delay the onset of migration (Marra et al. 1998), alter migratory routes, and even affect individual breeding performance (Ebbinge and Spaans 1995, Baker et al. 2004). Mortality rates during the migratory period can be 6–15 times higher compared to stationary periods (Sillett and Holmes 2002, Klaassen et al. 2014). Premigratory hyperphagia results in the accumulation of fat, protein, and other nutrients essential for migration (Newton 2008).

The Bobolink is a long-distance migratory, obligate grassland species that is known to forage extensively on rice (*Oryza sativa*) in South America prior to northbound migration (Pettingill 1983, López-Lanús et al. 2007, Renfrew and Saavedra 2007). Cultivated rice is a concentrated, abundant food resource. In regions of intensive rice production in Bolivia and Argentina, Bobolinks feed on rice when endosperm tissue forms (i.e. the late "milk stage" or "masoso" stage), 10–14 days before harvest (López-Lanús et al. 2007, Renfrew and Saavedra 2007). During southbound migration, Bobolinks have traditionally used coastal rice fields in the southern United States to convert carbohydrate-rich seeds into fat, earning them the nickname "butter birds" (Renfrew et al. 2015). In March, their energetic demands are elevated as they prepare for their 10,000 km northbound migration. Energetic demands also increase during periods of molt (Dietz et al. 1992, Murphy and King 1992), and the Bobolink is one of 2 bird species in North America known to undergo 2 complete molts each year (Howell 2010), including a prealternate molt on the wintering grounds from early January to mid-March (Renfrew et al. 2011). In Bolivia and Argentina, rice harvest extends from late January through late April. Bobolink molt generally begins before rice is widely available for consumption by Bobolinks (10–14 days before harvest; Pettingill 1983, Blanco et al. 2006, Renfrew and Saavedra 2007). Rice harvest begins by mid-molt and peaks in March–April (Blanco et al. 2006, R. B. Renfrew personal observation).

Linking winter diet and habitat use to breeding performance or location has been challenging for researchers (Webster et al. 2002). Feathers grown on the wintering grounds, and sampled on the breeding grounds, serve as intrinsic markers that allow inference of interseasonal connections. Replacement of flight feathers in Bobolinks during prealternate molt occurs sequentially over a 6–8 wk period (Renfrew et al. 2011). This species'

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unusual winter molt of flight feathers combines with its predominantly granivorous diet to provide a rare opportunity to examine its winter foraging ecology using stable carbon isotopes. Bobolinks have no visible fat during the prealternate molt (R. B. Renfrew personal observation); therefore, the feathers grown likely consist of nutrients obtained during the molt (Chamberlain et al. 1997, Hobson and Wassenaar 1997).

Stable carbon isotope ratios can be used to estimate the relative proportion of rice in the winter diet of Bobolinks by quantifying the C_3 vs. C_4 photosynthetic pathways (Féret et al. 2003). In southeastern Bolivia and northeastern Argentina, Bobolinks forage on grass seeds (Pettingill 1983, Di Giacomo et al. 2005, Renfrew and Saavedra 2007). In these lowland grasslands, C_4 plants dominate in species richness and percent cover (Cavagnaro 1988, Feldman et al. 2008). Rice has a C_3 photosynthetic pathway, which can be distinguished from C_4 plants in the diet of Bobolinks (Gealy 2008). Furthermore, the sequential nature of the prealternate molt allows an assessment of temporal patterns in winter diet by using different feather types (Dalerum and Angerbjörn 2005).

We used stable isotope mixing models in a Bayesian framework to determine the contribution of rice to the winter diet of Bobolinks during their prealternate molt. We used isotopic values from feather samples that were grown throughout the molt, collected from Bobolinks on the wintering grounds and from 3 populations across the breeding range. Our main objectives were to (1) validate the ability of carbon isotopes to distinguish rice vs. nonrice diets by analyzing feathers from wintering Bobolinks with known diets; (2) compare the proportion of C_3 vs. C_4 diet sources in feathers grown on the wintering grounds as an indirect measure of their reliance on rice during early, middle, and late prealternate molt; (3) determine whether the proportion of rice consumed during winter prealternate molt differed among Bobolink breeding populations; and (4) determine whether primary coverts could be used for stable isotope analysis instead of primaries as a less invasive way of sampling multiple feathers. We expected that Bobolink feathers grown while the birds were in rice-growing regions would reveal a greater proportion of rice in the diet compared to those grown in regions with little rice, thus validating our methods. We predicted that rice would be part of the Bobolink diet during all stages of the molt and consumed in greater proportions during late compared to early molt.

METHODS

Feather Sampling on the Breeding Grounds

In 2008, we captured Bobolinks breeding in Woodworth, North Dakota (47.13°N, 99.25°W), Shelburne, Vermont (44.38°N, 73.27°W), and Doniphan, Nebraska (40.8°N, 98.43°W), USA. In Vermont, our study sites consisted of 2 grass-based hay fields ~2 km apart (for a description of vegetation characteristics, see Perlut et al. 2006). The Nebraska site was composed of a mesic grassland and sedge meadow managed via prescribed burning and rotational grazing. In North Dakota, sites were located in the Woodworth Waterfowl Production Area, which consisted of remnant native prairie and formerly cultivated wetland and upland grasslands managed via burning and grazing.

We collected samples of feathers that were grown on the wintering grounds in South America from 105 adult male Bobolinks in Nebraska ($n = 30$), North Dakota ($n = 39$), and Vermont ($n = 36$) between May 16 and June 19 in 2008. We captured and banded male Bobolinks on their breeding territories in 2008 using mist nets and playback of conspecifics. The prealternate molt for each individual lasts a mean ($\pm$ SE) of 57 $\pm$ 3.5 and 44 $\pm$ 7.3 days in Bolivia and Argentina, respectively (Renfrew et al. 2011). Flight feathers on each wing molt synchronously (Ginn and Melville 1983), starting with the innermost primary (P1) and ending with the outermost secondary (S6) (Renfrew et al. 2011). For each captured male, we collected 2 cm of feather from the distal end of P5 on the left wing and P1 and S6 on the right wing. This provided isotopic values from the early (P1), middle (P5), and late (S6) stages of the prealternate molt, while balancing the potential effects of feather sampling over both wings.

Seed and Feather Sampling in Argentina and Bolivia

From 2006 to 2008, we captured Bobolinks using mist nets during the prealternate molt in 2 regions of their wintering grounds. In Bolivia, we captured Bobolinks at 4 sites (centroid = 15.761°S, 64.157°W; minimum and maximum distance between sites = 16 and 300 km, respectively) in February–March 2006 and in January 2007. These sites were located within areas of intensive rice production (Figure 1B) interspersed with fallow fields, extensive ranch land, and wetlands in Trinidad (Department of Beni) and in San Juan (Department of Santa Cruz). In Argentina, we captured Bobolinks at 2 sites in the humid Chaco in Santa Olga, Formosa Province (25.924°S, 58.535°W, distance between sites = 7.6 km), in January and February 2008. Sites in Argentina were in a landscape dominated by noncultivated upland grasslands with light grazing pressure, scattered marshes, limited sorghum production, and, to our knowledge, no rice production (Figure 1A). In Bolivia, we collected a rice sample ($n = 9$) from each different field where Bobolinks were observed feeding. In the few cases when we observed Bobolinks feeding on seed other than rice, we collected seed from the plant they were seen feeding on ($n = 7$; *Paspalum* spp., *Leptochloa* spp., and unidentified species).

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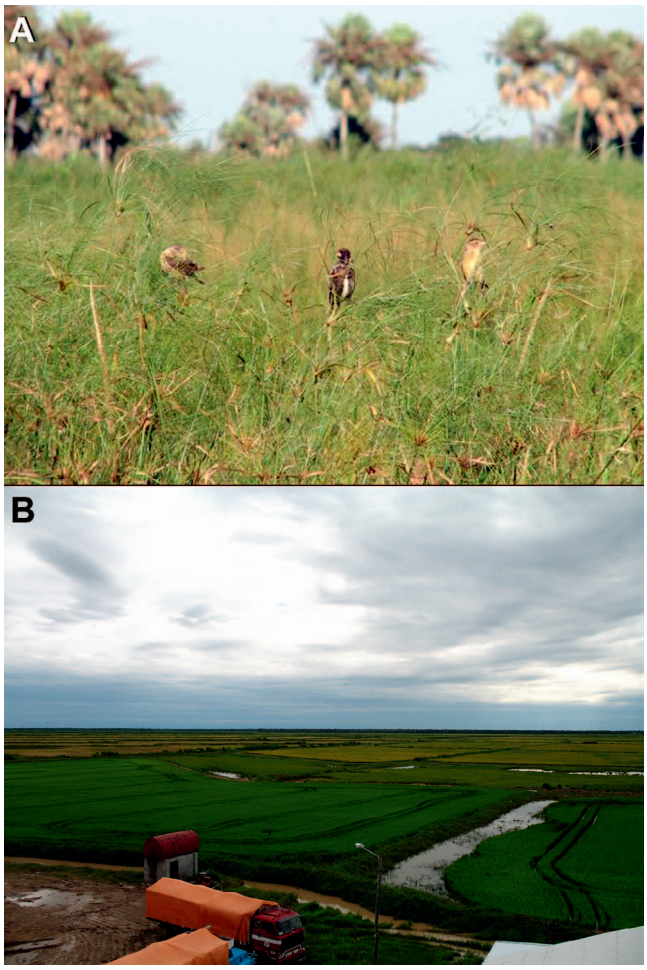


FIGURE 1. (**A**) Male Bobolink flanked by 2 female Bobolinks in grasslands of Formosa Province, Argentina. (**B**) Rice fields in the Department of Santa Cruz, Bolivia, where Bobolinks feed. Photo credits: Juan Klavins (A) and Rosalind Renfrew (B)

From each Bobolink captured, we collected 2 cm of an actively growing flight feather (Chamberlain et al. 1997, Hobson and Wassenaar 1997), and from some individuals ($n = 28$) we collected the entire most recently grown primary covert, to compare $\delta^{13}C$ values between primaries and primary coverts.

Stable Isotope Analysis

All stable isotope analyses were performed at the University of Georgia's Savannah River Ecology Laboratory. Feather samples were soaked in a 2:1 chloroform:methanol mixture for 24 hr to remove surface oils and internal lipids (Hobson and Welch 1992) and were rinsed with methanol and oven dried at ~45°C. Seeds of rice and of C_4 plants (*Sorghum* spp. and uncultivated grasses [Poaceae]) were hulled and crushed. Feather and seed samples were then weighed to the nearest microgram in a precleaned tin capsule. Capsules were then sealed and placed in the autosampler of a Carlo Erba Elemental Analyzer (NA 2500) attached to a continuous-flow isotope-ratio mass spectrometer (Finnigan Delta^{plus}XL) for carbon isotope analysis. Samples were converted to CO_2 in oxidation-reduction furnaces, separated by gas chromatography, and measured for carbon isotope composition on the mass spectrometer. An internal $CO_{2(g)}$ standard was used at the conclusion of each combustion for calibration to V-PDB international standards (Mariotti et al. 1980). External working standards of dogfish muscle and liver (assigned values of DORM-2: −16.94‰; DORM-3: −19.59‰) were analyzed after every fifth sample, and they were reproducible to <0.2‰ (±1σ SD) for carbon. The stable isotope ratio for carbon is expressed in standard delta (δ) notation compared to the international PDB standard (McKinney et al. 1950).

Statistical Analysis

We pooled $\delta^{13}C$ values of the C_4 plant sample analysis (*Sorghum* spp. and uncultivated grasses), because we were primarily interested in quantifying (1) the contribution of rice (C_3) vs. C_4 plants in Bobolink winter diets and (2) differences in rice consumption among breeding populations. Discrimination factors account for the difference in the isotopic values in an individual's tissue compared to its food sources (Olive et al. 2003), and it is important to account for these differences in stable isotope analyses (Phillips et al. 2014). We chose a feather-specific discrimination factor for $\delta^{13}C$ (+ 1.4 ± 0.6‰ [SD]) from a controlled study with quail that has a similar diet to Bobolink during winter (predominantly seed and some animal protein; Hobson and Clark 1992, Renfrew 2007, Blanco and López-Lanús 2008).

To compare the isotopic signatures of Bobolink feathers collected on both wintering and breeding grounds with winter food sources, we used stable isotope mixing models (SIMMs) in a Bayesian framework (Moore and Semmens 2008) in the MixSIAR graphical user interface (Stock and Semmens 2013). We used the samples from the flight feathers to compare the proportion of C_3 and C_4 sources in Bobolink diet. We processed the posterior distributions with Just Another Gibbs Sampler (JAGS; Plummer 2003) in R 3.3.2 (R Foundation for Statistical Computing, Vienna, Austria). For each model, we used noninformative priors and performed 100,000 iterations with 3 Markov chains, and discarded the first 50,000 iterations as "burn-in." We thinned iterations at a rate of 1:50 to reduce autocorrelation between posterior draws, and we retained 1,000 posterior distribution estimates per chain.

We treated *individual* as a random effect across all of our analyses involving the breeding populations to account for the repeated-measures nature of our sampling protocol. We were interested in the variation between populations, so we modeled it as a fixed effect. Also, we

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TABLE 1. Mean (± SD) proportions of rice (C_3) and C_4 plants consumed by 3 breeding populations of Bobolinks on their wintering grounds during the prealternate molt in 2008, with numbers of birds sampled (*n*) and 95% credible intervals (CrI).

		Rice		C_4 plants	
Study site	*n*	Mean	CrI	Mean	CrI
Nebraska	30	0.29 ± 0.04	0.21–0.37	0.71 ± 0.04	0.63–0.79
North Dakota	39	0.31 ± 0.03	0.25–0.38	0.69 ± 0.03	0.62–0.75
Vermont	36	0.27 ± 0.04	0.20–0.34	0.73 ± 0.04	0.66–0.80

compared the proportion of food sources (rice vs. C_4 plants) consumed on the wintering grounds between the 3 breeding populations and molt stages (early, middle, and late).

To determine whether $\delta^{13}C$ in feather samples from Bobolinks stem largely from the consumption of rice seeds, we used SIMMs to analyze $\delta^{13}C$ from actively growing Bobolink feathers in regions with and without rice production in Bolivia and Argentina. To demonstrate the validity of using coverts rather than primary feathers, we used a Bayesian paired *t*-test and correlation coefficient implemented in the BayesianFirstAid package (Bååth 2014) for $\delta^{13}C$ values of primary flight feathers and their associated coverts. Within the *t*-test, we deemed the results to be significant if the mean paired difference (between the $\delta^{13}C$ primary and covert values) did not overlap zero.

To assess model convergence, we examined trace plots of posterior distributions and the Gelman-Rubin (Gelman and Rubin 1992) test statistic ($\hat{R} \leq 1.05$). Results are presented as mean proportions (± SD) with lower and upper 95% credible intervals (CrI). Statistical significance of the results was derived by comparing posterior distributions, and differences were considered significant if the 95% CrI of $\delta^{13}C$ mean values did not overlap 1.0.

RESULTS

The mean $\delta^{13}C$ value was −29.84 ± 0.62 for C_3 rice ($n = 9$), and −13.75 ± 0.48 for C_4 grasses ($n = 5$) and sorghum ($n = 2$). Bobolinks in a rice-producing region in Bolivia ($n = 37$) had a diet dominated by C_3 material (68.5 ± 2.4%, 95% CrI: 63.7–73.2), with less of C_4 material (23.1 ± 2.8%, 95% CrI: 17.7–28.4). Conversely, Bobolinks ($n = 37$) captured in a region in Argentina with no known rice production consumed a greater proportion of C_4 material (0.77 ± 0.03, 95% CrI: 0.72–0.82) than of C_3 material (0.23 ± 0.03, 95% CrI: 0.18–0.28).

Across the 3 breeding populations, the winter diet consisted of 2.43 ± 0.29 (95% CrI: 1.93–3.07) times more C_4 than C_3 material. The proportion of C_3 (0.29 ± 0.02, 95% CrI: 0.25–0.34) and C_4 material (0.71 ± 0.02, 95% CrI: 0.66–0.75) in the diet was similar across all 3 breeding populations (Table 1). The winter diet of most individual Bobolinks (93.3%) from these breeding populations consisted of a greater proportion of C_4 material than C_3 material.

Bobolink C_3 material consumption was highest during the late stage of molt (Table 2). During late molt, Bobolinks consumed 1.57.9 ± 0.18 (95% CrI: 1.27–1.96) times and 1.89 ± 0.24 (95% CrI: 1.51–2.42) times more C_3 material compared to the early and middle molt stages, respectively. This pattern was driven by results from 2 of the 3 breeding locations (Figure 2). In North Dakota, during late molt, Bobolinks consumed 1.59 ± 0.23 (95% CrI: 1.21–2.09) times and 2.69 ± 0.60 (95% CrI: 1.84–4.16) times more C_3 material compared to the early and middle stages of molt, respectively. Similarly, the late-molt diet of Bobolinks breeding in Vermont consisted of 4.77 ± 2.38 (95% CrI: 2.38–10.65) times and 2.63 ± 0.67 (95% CrI: 1.70–4.27) times more C_3 material compared to the early and middle stages of molt, respectively.

The $\delta^{13}C$ values between a primary and its matching primary covert were correlated ($\rho = 0.88$, 95% CrI: 0.76–0.96, $n = 28$). The $\delta^{13}C$ values from the coverts tended to be more negative than those from the primaries, but this difference was small and not statistically different (mean paired difference = 0.25, 95% CrI: −0.32 to 0.74).

TABLE 2. Mean (± SD) proportions of rice (C_3) and C_4 plants consumed by Bobolinks from 3 breeding populations during the early, middle, and late stages of the prealternate molt on the wintering grounds in 2008 (approximately January–March), with numbers of birds sampled (*n*) and 95% credible intervals (CrI).

		Rice		C_4 plants	
Molt stage	*n*	Mean	CrI	Mean	CrI
Early	102	0.26 ± 0.03	0.19–0.32	0.74 ± 0.03	0.68–0.81
Middle	103	0.21 ± 0.03	0.16–0.27	0.79 ± 0.03	0.73–0.84
Late	104	0.40 ± 0.03	0.33–0.46	0.60 ± 0.03	0.54–0.67

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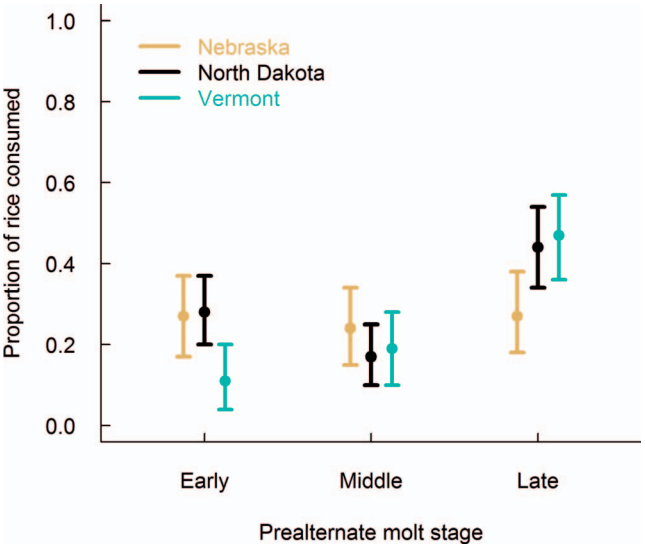


FIGURE 2. Proportions of rice consumed (with 95% credible intervals) by 3 breeding populations of Bobolinks during the early, middle, and late stages of the prealternate molt in 2008 (approximately January–March) in Nebraska ($n = 30$), North Dakota ($n = 39$), and Vermont ($n = 36$), USA.

DISCUSSION

Large flocks of wintering Bobolinks are regularly observed feeding in South American rice fields (Blanco et al. 2006, Renfrew and Saavedra 2007), but the extent to which the species relies on rice during austral summer remains largely unknown. Across 3 geographically distinct breeding populations, Bobolinks relied on C_3 sources for nearly one-third of their diet during the 6–8 wk prealternate molt. In our study, Bobolinks increased rice consumption just prior to northbound migration, which begins in late March and early April (Chapman 1890:198, Renfrew et al. 2013). Heavy reliance on rice during premigration hyperphagia could benefit birds by providing calories; or, alternatively, rice may lack important nutrients and its consumption can pose an increased risk of exposure to pesticides.

Rice seeds contain more carbohydrates and provide more metabolizable energy for ducks and geese compared to natural plant seeds (Miller 1987). However, rice seeds may lack essential amino acids, lipids, and protein found in natural plant seed, and they are lower in potassium, nitrogen, and calcium compared to most natural plant seeds (reviewed in Stafford et al. 2010). Compared to other cereal crops (e.g., corn [*Zea mays*] and sorghum), used less frequently than rice by Bobolinks during the austral summer (López-Lanús et al. 2007, Renfrew and Saavedra 2007), rice is a relatively low-fat and low-protein food (Ringelman 1991). Although more research is needed, studies have found that melanin production can be restricted by calcium (McGraw 2007) and the amino acid tyrosine (Poston et al. 2005) in the diet, even for achromatic feathers (Guindre-Parker and Love 2014). The effects of melanin on feather color may serve as a signal of body condition (e.g., Wiebe and Vitousek 2015). It is unknown whether Bobolinks with diets high in rice during molt may influence melanin and, subsequently, body condition and signaling. Cultivated rice may differ from other sources in other nutrients as well. For example, data collected for human nutrition indicate that wild rice (historically consumed by Bobolinks) contains 14.7 g protein and 1.1 g fat per 100 g, whereas white rice (currently consumed by Bobolinks) contains 7.1 g of protein and 0.7 g of fat per 100 g (U.S. Department of Agriculture [USDA] 2016). Bobolinks may supplement white rice with other, protein-rich foods to maximize molt efficiency (Murphy and King 1992). For example, wintering Bobolinks are known to consume some insects (Renfrew et al. 2015) and have been observed feeding on insects and grass seed between bouts of foraging in rice (Renfrew and Saavedra 2007).

The reliance on rice during the prealternate molt might help in identifying threats that contribute to the observed decline in Bobolink across the species' range. On the wintering grounds, flocks of thousands of Bobolinks consume rice within 2 wk of harvest, earning them pest status among rice growers (Renfrew and Saavedra 2007). In these regions, Bobolinks are exposed to lethal control by farmers and exposure to toxic pesticides intended for insect control when they feed in rice fields (Renfrew and Saavedra 2007, Parsons et al. 2010). In the past, rice farmers have used pesticides to intentionally kill flocks of Dickcissels in Venezuela (Basili and Temple 1999) and Bobolinks in Bolivia (Renfrew and Saavedra 2007). A recent study found that 40% of Bobolinks in rice production regions in Bolivia were exposed to organophosphates at sublethal or lethal levels (R. B. Renfrew et al. personal observation).

The availability of rice to Bobolinks in Bolivia and Argentina corroborates our findings. At the onset of the prealternate molt, the diet of all birds was predominantly C_4-based, but it dropped to ~60% C_4 by the end of the molt prior to northbound migration. Rice is not grown synchronously across the landscape; harvesting takes place across several months beginning in late January. To provide context for our feather isotope data, we compiled agricultural statistics (USDA 2006, 2011), data from other studies, and direct observations to illustrate the timing of Bobolink molt with the availability of rice in Bolivia and Argentina (Figure 3). As Bobolinks approach mid-molt in February, the edible, masoso-stage rice is more widely available. Bobolinks complete their molt around mid-March (Renfrew et al. 2011), early in the period of peak harvest and, presumably, when masoso-stage rice is most abundant.

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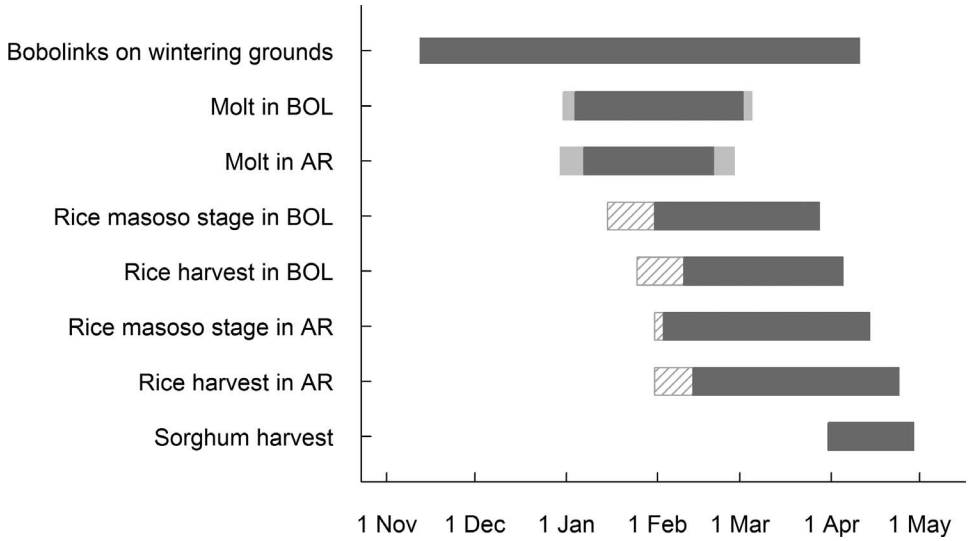


FIGURE 3. Duration (dark gray bars) with SE (light gray bars) of Bobolink molt and crop schedules in Bolivia (BOL) and Argentina (AR) (Renfrew et al. 2011). Masoso stage is when rice is in a soft form consumed by Bobolinks 10–14 days before harvest (Renfrew and Saavedra 2007, Blanco and López-Lanús 2008). Harvest schedules are approximations (USDA 2011) augmented with field observations (indicated by crosshatching; Blanco et al. 2006, R. B. Renfrew personal observation).

Populations of Bobolinks at our 2 northernmost sites (Vermont and North Dakota) demonstrated the greatest shift to a reliance on rice in the late stage of the prealternate molt, whereas rice consumption by Bobolinks breeding in Nebraska was constant throughout the molt. Geolocator data suggest weak or no migratory connectivity among Bobolinks and show that the species aggregates in areas of intensive rice production during the austral summer (Renfrew et al. 2013). The spatial resolution from light-level geolocators, however, prohibits evaluation of habitat use or diet composition to assess whether there are fine-scale movement patterns that could result in different diets among breeding populations.

Actively growing Bobolink feathers collected during austral summer in South America were 3 times higher in C_3 in a region of high rice production (Bolivia) than in a region without commercial rice production (Argentina). Based on this result and the low relative availability of C_3 grass seed at that time (Garbulsky and Deregibus 2004), we argue that although any amount of C_3 could be from consumption of rice, a conservative assumption is that a proportion of C_3 above the baseline (~20%) we found in Bobolinks occupying a region without rice likely indicates consumption of rice. This background proportion of C_3 above the baseline value (~20%) that was observed in the region without rice production may have resulted from undetected, small rice fields in the region, or from relatively long-distance movements of birds prior to capture (i.e. originating from a high-rice-production region). Also, it is possible for Bobolinks to consume seeds from C_3 sedges and shrubs, although this has been infrequently observed (Blanco et al. 2006, Renfrew and Saavedra 2007, Renfrew et al. 2015, R. B. Renfrew personal observation, G. Marino personal observation). A more likely source of baseline C_3 is from the consumption of insects that have fed on C_3 plants (e.g., sunflower [*Helianthus annuus*] and soybean [*Glycine max*]), given that Bobolinks do eat small amounts of insects during the nonbreeding season (Renfrew et al. 2015, Perlut and Renfrew 2016) and have occasionally been observed opportunistically eating insects while day-roosting in shrubs (R. B. Renfrew personal observation).

Land-use changes in South America—including a conversion of grasslands to crops (Baldi and Paruelo 2008, Killeen et al. 2008) and extensive annual burning of grasslands (Asociación Armonía 2012), in addition to the predicted impacts of climate change on primary productivity (Magrin et al. 2005)—indicate that the food resource will continue to change for bird species that forage in crops. The implications of these changes on a wintering long-distance migrant require an understanding of the interactions between diet, energetic requirements, and body condition. Our study shows that Bobolinks rely most heavily on uncultivated food sources during the winter molt. This species' propensity to travel across large areas and its somewhat plastic diet (Renfrew 2007) suggest that it may be resilient to changes in foraging opportunities. The net consequences of fewer grasslands and more croplands could be positive (e.g., highly concentrated, high-calorie food source) or negative (e.g., decrease in nutrition, increased exposure to pesticides), and studies of the nutritional and toxicological effects of various

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treatments during molt and premigration hyperphagia are needed.

Maintaining grasslands and their seeding phenology will continue to provide the grass seed that our results suggest Bobolinks rely upon more than any other food resource. Where application of highly toxic pesticides occurs, promoting Integrated Pest Management programs focused on reducing pesticide applications during March and early April would reduce exposure risks to Bobolinks. Instead of combating rice seed predation by Bobolinks using scare tactics that move the birds from field to field, farmers may elect to "sacrifice" one field (a "trap field") to Bobolinks, which can prevent them from foraging in other fields. A farming community can even choose to collectively compensate the farmer who provides the trap field. Most of these measures would contribute to the conservation of a suite of resident and migratory grassland bird species in South America that forage in rice and depend on grassland habitat.

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