BIODIVERSITY RESEARCH

Phenological matching across hemispheres in a long-distance migratory bird

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ABSTRACT

Aim In the Northern Hemisphere, bird migration from the tropic to the temperate zone in spring is thought to proceed at a rate determined in large part by local phenology. In contrast, little is understood about where birds go or the factors that determine why they move or where they stop during the post-breeding period.

Location Study sites were in Oregon, Nebraska and Vermont, and location data we collected extend south to Argentina.

Methods We deployed light-level geolocators on individual Bobolinks from three populations across the breeding range and compare their southbound movement phenology to austral greening as indicated by the Normalized Difference Vegetation Index.

Results Bobolinks from all breeding populations synchronously arrived and remained for up to several weeks in two sequential, small non-breeding areas that were separated by thousands of kilometres, before staging for pre-alternate moult. Similar to the migration patterns of birds to northern breeding areas, movements into the Southern Hemisphere corresponded to increasing primary productivity.

Main conclusions Our findings suggest that the Bobolink's southbound migration is broadly constrained by resource availability, and its non-breeding distribution has been shaped by the seasonal phenology of grasslands in both time and space. This is the first documentation of individual birds from across a continental breeding range exhibiting phenological matching during their post-breeding southward migration. Known conservation threats overlap temporally and spatially with large concentrations of Bobolinks, and should be closely examined. We emphasize the need to consider how individuals move and interact with their environment throughout their annual cycle and over hemispheric scales.

Keywords
Bobolink, *Dolichonyx oryzivorus*, geolocators, migration phenology, migratory connectivity, Normalized Difference Vegetation Index.

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INTRODUCTION

How and why animals migrate and disperse over space and time is a poorly understood yet fundamental aspect of animal ecology (Nathan *et al.*, 2008). These questions have remained challenging for small animals that occupy vast spatial areas because the technologies for tracking their movements have been unavailable. How populations across a migratory species' breeding range disperse, migrate or otherwise move after the breeding season remains unknown. Equally lacking is an understanding of the factors that drive the timing and sequence (i.e. phenology) of movements in animals. It is assumed that these behaviours are often timed to take advantage of optimum resource availability and to

maximize fitness, but few direct data are available to support these theories (Nathan *et al.*, 2008).

Our ability to answer questions involving the movement of individual animals and patterns of distribution over large spatial scales is rapidly changing because of recent developments in tracking technology (Webster *et al.*, 2002). Such improvements, including the use of stable isotopes of hydrogen (Studds *et al.*, 2012), and the miniaturization of light-level geolocators and satellite transmitters allow scientists to track the movements of small animals over their full life cycle (Robinson *et al.*, 2010; Bridge *et al.*, 2011). Using such year-round location data from individuals allows researchers to explore how local factors such as temperature and wind influence movements (e.g. Åkesson *et al.*, 2011; Schmaljohann *et al.*, 2012) and to suggest whether movements may be governed by endogenous versus exogenous factors (e.g. Tøttrup *et al.*, 2012). Most importantly, these technologies facilitate the study of key ecological factors that underlie movements of individual small animals over large spatial scales. For the first time, research can address new fundamental questions regarding animal ecology and evolution (Webster & Marra, 2005) and better inform issues critical to conservation (Marra *et al.*, 2011).

For songbirds, the degree to which resource availability and movement dynamics influence patterns of migratory connectivity is completely unknown. *Migratory connectivity* is the geographical linking of bird populations between different stages of their annual cycle, including breeding, migration and winter (Webster *et al.*, 2002; Marra *et al.*, 2006). Little information exists about how populations are geographically connected throughout the annual cycle. Year-round ranges have been known for many species, but not the routes taken by individuals or populations or the endpoints. As a result, the limiting factors and regulatory mechanisms that impact animal populations throughout the annual cycle are poorly understood (Marra *et al.*, 2006; Newton, 2008). Understanding migratory connectivity is key to interpreting fundamental ecological and evolutionary patterns, managing environmental challenges like oil spills or climate change and predicting and addressing known threats such as the spread of zoonotic diseases, bird collisions with aircraft and the positioning of alternative energy structures (Marra *et al.*, 2006).

Similarly, we know little about the factors that govern movement (Nathan *et al.*, 2008), especially for small passerine songbirds. Part of the problem is that research has largely relied on indirect measures (e.g. band recoveries, genetic and isotopic markers) or site-specific data during a short time frame to describe movements and their drivers and has not followed individuals through the entire migration or annual cycle. Such studies have often linked population effects and described changes in movements over decades or longer. For example, the amount of precipitation on non-breeding areas has been correlated with winter habitat quality for migratory birds (Møller, 1989; Peach *et al.*, 1991; Szép, 1995a,b; Saino *et al.*, 2004), and this has been shown to be tightly linked to the timing of departure (Studds & Marra, 2011) and arrival on breeding areas (American Redstart [*Setophaga ruticilla*]: McKellar *et al.*, in press; Kirtland's Warbler [*Setophaga kirtlandi*]: Rockwell *et al.*, 2012). Earlier arrival of Palaearctic–African migrants onto breeding areas in Europe has also been associated with warmer temperatures (Both *et al.*, 2005; Tøttrup *et al.*, 2008) and primary productivity (Balbontín *et al.*, 2009) on spring migratory staging grounds, suggesting that events during migration impede or assist migration. Post-breeding, how resource availability or its proxies affect fall migration has received little attention (for general considerations, see Salewski & Jones, 2006). Direct evidence showing the migratory movements of individual songbirds relative to resource availability is lacking for any species or migration system. Progress in this arena has been impeded in part by the inherent difficulty of simultaneously tracking individual animals, along with the resources they depend, over landscape scales.

Plant phenology is a central determinant of resource availability, either directly or via influences on prey emergence and abundance (Visser & Both, 2005). Remotely sensed, spatially explicit indices of 'greening' or primary productivity (Schwartz, 1998) have also been compared with animal movement data to better understand how plant phenology might influence the timing of animal migration (e.g. Marra *et al.*, 2005; Tombre *et al.*, 2008; Sawyer & Kauffman, 2011). The 'green wave hypothesis' predicts that avian herbivores such as waterfowl follow plant emergence and growth along their spring migration route (Drent *et al.*, 1978; Owen, 1980), and this primary productivity is considered the main force driving migration rates for avian herbivores (Van der Graaf *et al.*, 2006; van Wijk *et al.*, 2012). Such patterns have also been shown for songbird species: warmer temperatures stimulate budburst, and this has been indirectly correlated with the rate of spring migration (Marra *et al.*, 2005). Demonstrating such relationships for individual birds over broad geographical scales and finer time frames has thus far been impossible.

The Bobolink (*Dolichonyx oryzivorus*) has one of the longest migrations (*c.* 20,000 km round trip) of any songbird in the world. Its migration phenology, migratory spatial patterns and population connectivity remain unknown. As a 'niche-follower' (Nakazawa *et al.*, 2004), the Bobolink occupies open agricultural and non-agricultural grasslands on both its breeding territories in North America and on its non-breeding grounds in South America. During the non-breeding period, foraging flocks in agricultural fields may number in the thousands to tens of thousands, earning the species pest status in farmlands (López-Lanús *et al.*, 2007; Renfrew & Saavedra, 2007; Blanco & López-Lanús, 2008). Its apparently patchy distribution during the non-breeding season makes the Bobolink potentially vulnerable to localized threats such as pesticide applications. Determining the magnitude and extent of such threats on survival and productivity, and ultimately their contribution to population dynamics, requires an understanding of the species'

migratory connectivity (Marra *et al.*, 2006) along with the phenology of its movements and the mechanisms that drive those patterns at a hemispheric scale and throughout the year.

Miniaturized light-level geolocators now provide a means to track movements of individual songbirds year-round, allowing spatially explicit assessments of how stopover and wintering site characteristics shape migration schedules (Bridge *et al.*, 2011). We deployed light-level geolocators on Bobolinks from three distinct populations across the continental breeding range (Oregon, Nebraska, Vermont) to assess the strength of their migratory connectivity, patterns of movement and the ecological factors that govern movements. To determine how large-scale movements coincide with primary productivity, we compared the spatial and temporal migration patterns of these Bobolinks in South America with patterns of primary productivity as indicated by the Normalized Difference Vegetation Index (NDVI; Myneni *et al.*, 1995). The Index is strongly correlated with rainfall (Davenport & Nicholson, 1993) and has been used successfully to indirectly identify important bird wintering and migration grounds (Szép & Møller, 2005) and to associate stopover and winter habitat quality with arrival to breeding grounds (Saino *et al.*, 2004; Tøttrup *et al.*, 2008; Balbontín *et al.*, 2009) and population abundance (Wilson *et al.*, 2011). If Bobolinks are matching the phenology of primary productivity, we would expect to find a) a decrease in NDVI between arrival and departure times at a stop or b) movements from lower to higher NDVI.

METHODS

We captured Bobolinks in north-western Vermont (VT; N44°23′, W73°16′), along the Platte River in south-eastern Nebraska (NE; N40°48′, W98°26′), and at Malheur National Wildlife Refuge in Princeton, OR (OR; 43°16′N, 118°50′W) by placing mist nets strategically in areas of relatively high Bobolink density or near known nests with chicks. In 2009, we attached 1.2 g Mk-10 geolocators developed by the British Antarctic Survey (BAS) to 15, 20 and 10 males in VT, NE and OR, respectively (*n* = 45). Light sensors were located at the tip of a 15-mm stalk that rose above the backpack unit at a 30° angle. We used a leg loop harness system (Rappole & Tipton, 1991) with Kevlar 400-lb thread (total mass = 1.3 g). In 2010, we deployed 0.9 g Mk-12 (BAS) geolocators on 20 Bobolinks at each of the same three sites (*n* = 60). Eight of the geolocators were deployed on females in VT and in OR. We used a Teflon 0.1-wide ribbon for a harness (total mass = 1.0 g).

In 2010, we retrieved four geolocators: two in VT and two in NE. One of the geolocators from NE failed for unknown reasons soon after deployment. In 2011, we recovered 13 geolocators (four in OR, seven in NE, two in VT); one NE geolocator contained no data (lost stalk). Batteries from geolocators retrieved in 2011 died between 31 January and 8 May 2011.

We processed light data from 15 recovered geolocators and obtained point location estimates using BAS software (BAST-rak suite, Cambridge, UK). Light curves around sunrise and sunset from an open-habitat species like Bobolink are extremely 'clean', and we were able to easily identify aberrant curves; these days were deleted (Phillips *et al.*, 2004). Latitude estimates within 15 days of the fall (21 September) and spring (21 March) equinox were not used. This resulted in latitude data being removed for dates ranging from 1 September to 13 October and from 2 March to 8 April for fall and spring equinox, respectively. These and other shading events resulted in deletion of 97 days (2% of the 3924 days not used for calibration) for all geolocators (mean = 6.5, range = 1–21 days). During periods influenced by an equinox, we determined significant migratory movement based on consistent, long-term ($\geq$ 3 days) or permanent short-term longitudinal changes $\geq$ 2 decimal degrees. We deleted points > 500 km from any other point in areas where a bird was stationary [total of 17 days (0.4%) for all geolocators].

Geolocators provide both noon and midnight position fixes. To minimize error, we used fixes when an individual is assumed to be stationary. During the non-breeding season, Bobolinks may change their roost location during the day (Renfrew & Saavedra, 2007); we used only midnight locations during these periods. Bobolinks are generally nocturnal migrants, but transoceanic flights may include diurnal flights. We assumed that Bobolinks also move during the day; we used both noon and midnight positions during migratory flights and estimated the bird's true location at the midpoint between noon and midnight fixes.

We calibrated data from each geolocator using the first 7–10 days after the deployment, when the birds were at a known location (on territory). Bobolinks inhabit open grasslands throughout the year, and we assumed that influences of vegetation density and weather on shading were consistent throughout deployment. We assumed no significant differences in behaviour or habitat at dawn and dusk (changing the amount of typical light attenuation) at the breeding site compared to the rest of the year.

We evaluated geolocator accuracy by averaging the recorded positions while birds were on breeding territories (i.e. until fall migration movement was evident). Latitudinal error ranged from 18 to 271 km (mean = 132 ± 20.3 km), and longitudinal error ranged from 2 to 36 km (mean = 16 ± 2.7 km). Potential sources of error include variation in logger light sensitivity, individual behaviour during sunrise and sunset, cloud cover and weather and differences among territories in topography (Lisovski *et al.*, 2012). It is likely that on average, error is overestimated because individuals often make local movements upon completion of breeding in July. However, individuals also move locally during the non-breeding season (Renfrew & Saavedra, 2007), so this source of error, though likely variable in its magnitude, may apply throughout the year.

For stays in one area $\geq$ 20 days, we calculated kernel density estimates that encompassed 50%, 75% and 90% of

the maximum density (ESRI, 2010). We set cell size and search radius at 2 and 270 km (to encompass point estimates within the maximum known error at breeding locations; Bächler *et al.*, 2010), respectively. We estimated total area used by Bobolinks on polygons of combined 90% kernels for all birds. Kernels were displayed on maps as a winter staging site if a bird was arrived $\geq$ 1 December or the bird remained in the area past 1 January. Significance was evaluated at α = 0.05, marginal significance at α = 0.10, and multiple tests were corrected using a Bonferroni adjustment. To make general comparisons between the total area of the breeding range versus the non-breeding areas in South America, we created polygons in ArcMap (ESRI, 2010) to outline the regions depicted by the Breeding Bird Survey (Sauer *et al.*, 2011) and composites of the 90% kernels for stops, respectively.

Within 90% composites, we calculated biweekly average (2000–2012). Normalized Difference Vegetation Index (NDVI) using a standardized dataset corrected for calibration, view geometry and volcanic aerosols (MODIS 16-day NDVI, 10-km resolution; Huete *et al.*, 1999). NDVI is a measure of the amount and vigour of vegetation on the land surface based on the level of photosynthetic activity. The finest temporal scale available for NDVI data was biweekly; we calculated the midpoint for each 2-week interval for plotting and analysis. To evaluate habitat conditions on stopover and wintering areas, we used land cover classification data to clip NDVI averages from 2003 to 2012 to areas within Bobolink 90% kernel location estimates, classified as 'periodically flooded savanna', 'grass savanna' and or 'intensive agriculture' (Bartholomé & Belward, 2005). To assess associations between higher levels of flooding and NDVI in Bolivia, we examined the relationship between NDVI and a satellite-derived measure of water accumulation within the natural savanna areas defined by Bobolink kernel distributions. Monthly satellite data for water accumulation were obtained land water content estimates (NASA, 2012), which are related to the movement of surface and groundwater across landscapes (Tapley *et al.*, 2004).

RESULTS

Non-breeding spatial and temporal convergence

After leaving breeding areas in Oregon, Nebraska and Vermont, USA, in autumn, 15 Bobolinks (13 males, two females) with light-level geolocators converged spatially at 2–4 sequential non-breeding areas (Fig. 1). From a breeding range of *c.* 5,625,000 km^2, all birds migrated in autumn through the Caribbean, converged longitudinally to stop within a 530,000 km^2 area (one-tenth the size of the breeding range) in northern Venezuela (and eastern Colombia, hereafter referred to as Venezuela; 327,000 km^2 in open habitat) and continued onto a 460,000 km^2 area in Bolivia. All 15 Bobolinks with geolocators occupied an area

< 2,000,000 km^2 during December-March; of those, the 12 birds that staged in Argentina were in a 616,000 km^2 area – one-ninth the size of the breeding area.

The tight spatial convergence of Bobolinks during the southbound migration was accompanied by strong temporal synchrony (Fig. 1). Despite individual variability in arrival and departure dates at non-breeding areas, mean dates at non-breeding areas were nearly exact among breeding populations (Fig. 2). The longest stops were at the southernmost areas, where Bobolinks are known to stage for their pre-alternate moult, during which they replace non-breeding body and flight feathers with the feathers that make up their breeding plumage. Two years of data from the same individual showed variability in timing but fairly stable distribution between years (see Fig. S1 in Supporting Information).

Despite the synchrony of Bobolink occurrence in Venezuela and Bolivia, the number of days between departure from breeding grounds and arrival on winter staging/moulting grounds (Table 1) was greater for Oregon Bobolinks compared to birds breeding in Vermont (Mann–Whitney $U = 15$, $P = 0.08$) and Nebraska ($U = 0.0$, $P = 0.02$, $n = 7$). Oregon birds tended to leave breeding grounds earlier than birds breeding in Nebraska or Vermont. Oregon birds took longer to migrate to Venezuela compared to Nebraska birds ($U = 0$, $P < 0.01$) but not Vermont birds ($U = 9.5$, $P = 0.77$). It is possible that in some cases, estimated departure date was later than the actual date for Vermont and Nebraska, if initial movements away from the breeding grounds were only latitudinal and not detectable near the fall equinox. Three of the birds from Oregon showed clear eastward movement past the Rocky Mountains before the equinox affected latitude estimates (> 20 days from 21 September), before continuing south to the Caribbean (see Fig. S2). For all 15 Bobolinks, we found no correlation between date of departure from breeding grounds and date of arrival on winter staging grounds (Pearson's $r = 0.08$).

Spring departure was highly synchronous (3–8 April; $n = 4$; 11 batteries failed during winter) regardless of staging location. Spring migration lasted 5–6 weeks ($n = 3$). Stopovers were brief (< 1 week) and often bounded by lengthy flights (see Fig. S3). Individuals travelled different routes until they reached northern Columbia or Venezuela, where they converged spatially and for two birds (1 from Vermont, 1 from Nebraska), also temporally. The average rate of flight for the entire 9000–9500 km migration was 210–260 km per day including stopovers and 1000 km per day between stopovers. The fastest flight was a 1900-km transoceanic leg from Venezuela to the Bahamas within 1 day (79 km h^{-1}), undoubtedly assisted by tailwinds.

Synchrony of movements with primary productivity

Bobolink movements directly corresponded with increasing primary productivity, as measured by NDVI, in natural grasslands but not agricultural lands in the Southern Hemisphere (Fig. 3a,b). When Bobolinks arrived in Venezuela,
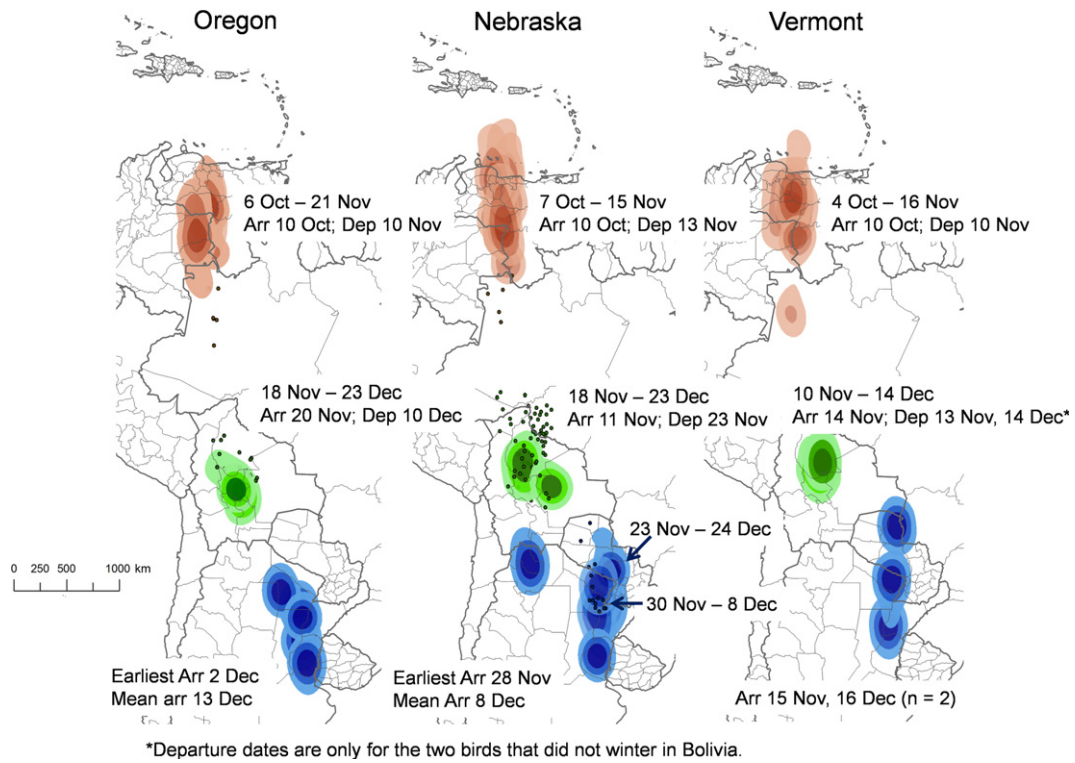
Figure 1 Non-breeding, stationary areas for Bobolinks breeding in Oregon (*N* = 4), Nebraska (*N* = 7) and Vermont (*N* = 4). Kernel density estimates, calculated for stopovers > 20 days, encompass 50%, 75% and 90% of the maximum density, from darkest to lightest colours, respectively (brown = Venezuela, green = Bolivia, blue = Argentina/Paraguay). Daily locations of birds during stops less than 20 days are represented by dots. Dates associated with each area are range of arrival and departure (top) and mean arrival and departure date (bottom). Datum WGS 1984.
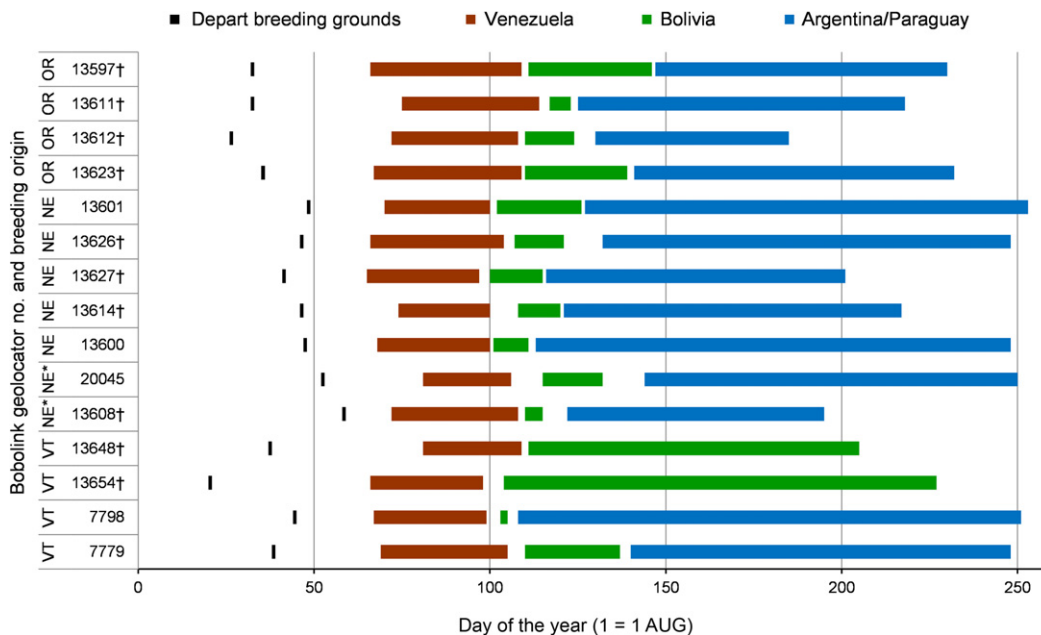

Figure 2 Timing of movements in South America for Bobolinks breeding in Oregon (OR), Nebraska (NE) and Vermont (VT). Geolocators 7779, 7798 and 20045 are data from 2009–2010, all others are 2010–2011. *same individual. †geolocator stopped operating on wintering grounds due to battery failure.

Table 1 Mean (SE) days of flights and stops in southbound migration of Bobolinks 2010–2011

Breeding	N	Depart breeding	Flight to VZ	VZ stop	BOL stop	Total migration
VT	4	20-August to 13-September	35 (5.5)	33 (1.6)	3, 28*	79 (8.0)
NE	7	10-September to 27-September	22 (1.9)	33 (2.3)	15 (2.3)	75 (3.8)
OR	4	26-August to 4-September	38 (3.5)	41 (1.6)	22 (6.8)	108 (4.5)
All	15	20-August to 27-September	29 (2.6)	35.2 (1.5)	17 (2.8)	85 (4.9)

VT, Vermont; NE, Nebraska; OR, Oregon; VZ, Venezuela; BOL, Bolivia; AR, Argentina.
*Two birds remained in BOL for entire winter.
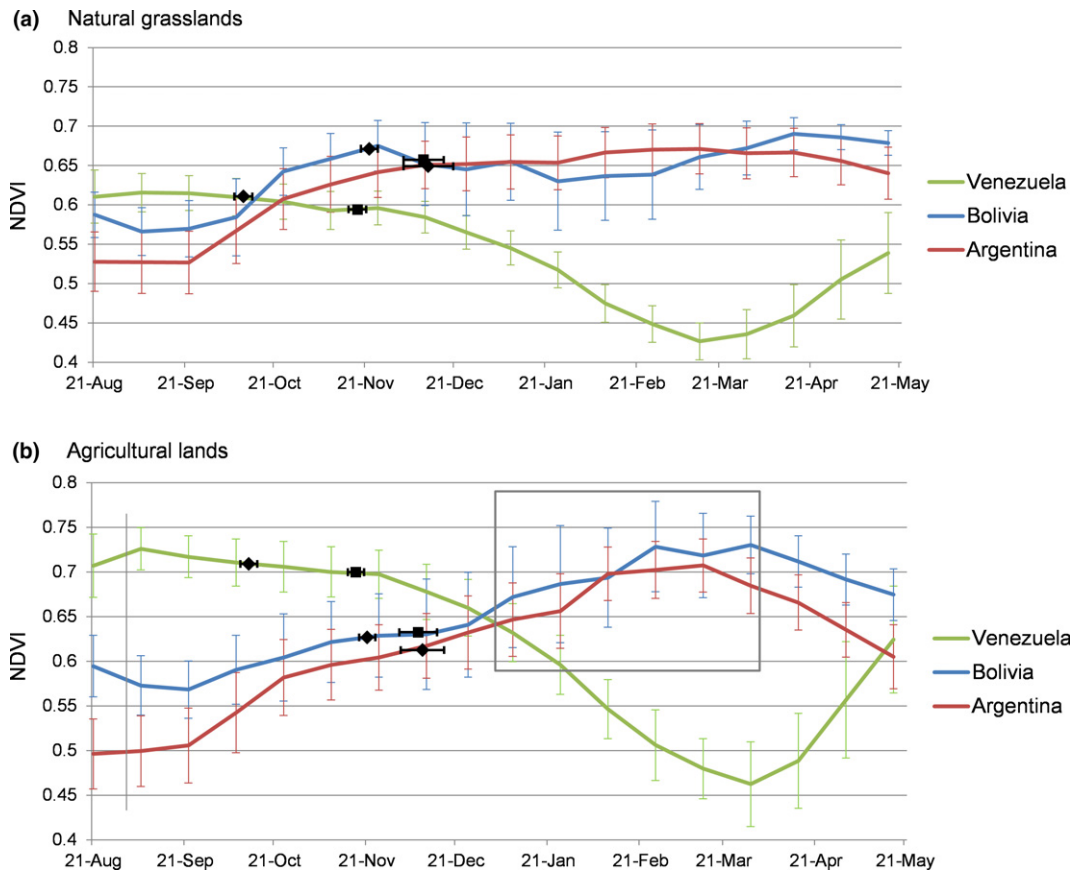
Figure 3 Normalized Difference Vegetation Index (NDVI; lines) within 90% kernels of Bobolink non-breeding locations. Mean arrival (diamonds) and departure (squares) dates of Bobolinks for each location with 95% CI are in black. The grey rectangle in (b) indicates approximate period when rice is available to Bobolinks in Bolivia and Argentina (Renfrew & Saavedra, 2007).

grassland NDVI was higher than levels on the breeding grounds when Bobolinks initiate migration (e.g. in Flint Hills KS, 2001–2005 average NDVI for 1 September = 0.55; Gu et al., 2007). With the approach of austral spring, NDVI in Venezuela for both grasslands and agriculture was near peak levels through late November and then declined sharply through mid- to late March. As natural grassland NDVI declined in Venezuela, it increased in Bolivia and Argentina. The concomitant decline of primary productivity in natural grasslands in Venezuela and increase in Bolivia and Argentina corresponded with Bobolink movements from Venezuela, resulting in an 'upgrade' to regions with higher productivity. Bobolinks arrived in Bolivia in November, as

grassland primary productivity reached near-peak levels (Fig. 3a) that were higher than in Venezuela that month ($t = -12.8$, df = 23, $P < 0.001$). In contrast, NDVI of agricultural lands was lower in Bolivia compared to Venezuela at that time. During the period when rice is in the appropriate stage of seed formation (Renfrew & Saavedra, 2007) to be exploited by Bobolinks in Bolivia and Argentina, NDVI is higher in agricultural lands than in natural grasslands (Fig. 3b). NDVI was more variable in Bolivia compared to Argentina in January (Fig. 3a,b) due to high precipitation in 3 of 12 years (see Fig. S4) that caused higher water accumulation (flooding), resulting in lower NDVI ($R^2 = 0.581$, $F_{(1,9)} = 9.713$, $P = 0.017$).

DISCUSSION

Spatial and temporal convergence onto non-breeding areas

Bobolink breeding populations from across the North American continent converged temporally (within days of each other) and spatially into an area one-tenth the size of the breeding range in Venezuela during the non-breeding season. In a pattern that coincided with increasing vegetation productivity, all individuals then synchronously left Venezuela to fly south to Bolivia and most then continued onto Argentina where they undergo a complete feather moult prior to spring migration back to the breeding grounds.

The extraordinary migration pattern we report for the Bobolink includes some characteristics shared by a few Nearctic–Neotropical and Palaearctic–African migratory birds. Longitudinal range compression during migration, where populations emanating from a broader breeding range dramatically funnel through narrow geographical features, is seen in raptors, storks, pelicans and other large, soaring species. For example, Levant Sparrowhawk (*Accipiter brevipes*; Yosef, 2003) and Lesser Spotted Eagle (*Aquila pomarina*; Meyburg *et al.*, 1995, 2004) travel along very narrow routes for part of their journeys as they cross a land bridge between Asia, Africa and Europe. This pattern is less common in songbirds, but is seen, for example, with migrants originating from Western Europe converge at the eastern end of the Mediterranean Sea to enter Africa near the Nile River (Newton, 2008). Banding data indicate that Marsh Warblers are among the species to migrate southward along a very narrow corridor, passing through Kenya on a front only 100–200 km wide. Bobolinks use the Caribbean Islands as stepping stones between North and South America, channelling into a relatively small geographical area for that part of their journey, during both spring and fall. Most species of migratory birds that exhibit longitudinal compression during migration then expand to a broader wintering range, producing an hourglass pattern for their year-round range (Newton, 2008). This is seen in most Palaearctic–African migrants, although the majority (69%) of those species still maintains larger breeding ranges than wintering quarters. The compaction of the Bobolink winter range compared to the breeding range that we report is greater than for most songbirds, with the exception of species such as Lesser Grey Shrike (*Lanius minor*), which has a wintering range one-seventh the size of its breeding range (Newton, 1995).

Our study is one of the first to assess the strength of migratory connectivity of a long-distance migratory songbird from across the species' breeding range using tracking technology. Surprisingly, our data reveal extreme mixing of populations (i.e. weak connectivity) during the non-breeding season. Such a pattern suggests that the strength of natural selection during the non-breeding season will be equal across individuals regardless of breeding origin (Webster & Marra, 2005). Fine-scale connectivity (i.e. birds breeding in the same field that also flock together in winter), however, may not be detectable using geolocator data because of error inherent in light-level-based spatial location estimates. To better understand whether such fine-grain patterns of migratory connectivity exist in this species, additional research on the wintering grounds investigating patterns of habitat segregation (i.e. by sex, age or breeding origin) is needed. Other studies of migratory songbirds with broad longitudinal breeding ranges have reported strong migratory connectivity (e.g. Ryder *et al.*, 2011); however, most use stable isotopes or genetic methods, which have limited spatial resolution (e.g. eastern and western populations winter in different areas; Kimura *et al.*, 2002; Clegg *et al.*, 2003; Lovette, 2004; Boulet *et al.*, 2006). To our knowledge, neither genetic nor isotope methods have been used to assess connectivity of Bobolink populations.

The mixing of disparate Bobolink breeding populations in South America during the non-breeding season may be driving and reinforcing the tight temporal synchrony we found among birds in South America. The synchrony of autumn stops, particularly in Venezuela, was remarkably high, especially given the different routes, years of data and distances travelled. Birds departed the breeding grounds to move away from less favourable conditions (decline of local food resources) and may have modulated the pace of their migration to match conditions (e.g. favourable weather, food resources) that resulted in their synchronous arrival in Venezuela. Oregon Bobolinks covered more distance but departed breeding grounds earlier, and Nebraska birds left the breeding grounds later, but travelled at a faster pace. The different strategies that resulted in synchronous arrival in Venezuela suggest selection for arrival date. Once birds converge in Venezuela, perhaps their timing of movement is to some degree endogenous and also modified by environment. The timing of their departure from Venezuela to continue southward would be under the same selective pressures, resulting in the synchrony across years. Synchronous departures are also likely facilitated and reinforced by social behaviours in this flocking species.

Regardless of how patterns of Bobolink movements developed, the high degree of spatial and temporal synchrony in Bobolink movements suggests that populations are strongly influenced by events outside of the breeding season. Food may be the most important limiting factor determining the distribution and abundance of birds during the non-breeding season (Sherry *et al.*, 2005). The unique distribution we found for Bobolinks was likely driven by patchy, limited food resources – specifically, crops and grasslands that provide seed for this primarily granivorous species. The clustered distribution of Bobolinks in South America illustrates how patchy food supply underlies their distribution: where crops such as rice and sorghum provide ephemeral, super-abundant resources, Bobolinks concentrate into large flocks, whereas the more diffused seed resources supplied by non-cultivated grasses, including grazed lands, support smaller,

more dispersed flocks (Renfrew & Saavedra, 2007; Blanco & López-Lanús, 2008).

No single word or phrase sufficiently describes the pattern of Bobolink movements that we report. Movements during the entire annual cycle of the Bobolink between breeding and wintering grounds can be characterized as continual, with occasional stops lasting no more than two months. Stops in Venezuela and Bolivia are likely essential staging areas that allow Bobolinks to complete their migration to Argentina, where they spend the majority of the winter months and undergo a pre-alternate moult (Renfrew et al., 2011). That the stops are often lengthy could suggest that energy gain per unit intake is quite low for a species eating primarily seeds.

Phenological matching

Our data suggest that Bobolinks moving into the Southern Hemisphere are matching large-scale movements to changes in primary productivity. This is an unparalleled, direct documentation of individual bird movements during the non-breeding season corresponding with austral greening. As with other migratory birds that breed in North America, Bobolink departure from breeding areas coincides with overall declines in primary productivity. During the month that Bobolinks remained in Venezuela, primary productivity began declining. Meanwhile, NDVI was rapidly increasing at the next major destination, the grasslands of Bolivia some 2000–2500 km south of Venezuela. When Bobolinks moved from Venezuela to Bolivia, they experienced a 12% mean increase in non-agricultural grassland NDVI. At that time, NDVI was slightly lower in Argentina than in Bolivia, but the majority of birds that then moved onto Argentina did so precisely when the mean NDVI there began to exceed that of Bolivia. The higher NDVI in Argentina from late December until late March, however, is not significant, suggesting there may be other reasons why most Bobolinks expend the energy to fly another 1000–2000 km to Argentina.

The high variability in Bolivia NDVI is likely due to standing water during high-precipitation years associated with El Niño–Southern Oscillation (ENSO), resulting in a less predictable food resource compared to Argentina. Widespread inundation is a regular phenomenon just east of the Andes in Bolivia (Ronchail et al., 2005), where most Bobolinks are found during austral summer (Renfrew & Saavedra, 2007), with up to 52% of the land flooded (Hamilton et al., 2004). During wet years, inundations reduce food resources available to Bobolinks at the time when they undergo a complete moult (late January–early March; Renfrew et al., 2011) and physiologically prepare for a rapid, 5- to 6-week migration to the breeding grounds. Both activities are energetically demanding and can be delayed by inadequate food supplies (Merilä, 1997; Rubolini et al., 2002; Saino et al., 2004; Newton, 2008). Flood-induced interruptions in food supply in Bolivia may not provide the predictable food resource required to support the energy demands of moult and preparation for spring migration. That 2 of 15 individuals still remained in Bolivia suggest that there may be trade-offs between expending more energy to reach areas of predictable productivity versus remaining in an area where there is a risk of not successfully locating adequate food resources. Alternatively, a proportion of birds may find local areas in Bolivia with sufficient resources regardless of annual variation in precipitation.

The Bobolink has a unique life history characteristic that may make the timing of its movements and its association with primary productivity singular among Nearctic–Neotropical songbirds: it is the only transequatorial migratory bird that is granivorous during the austral summer. At least some populations of insectivorous species such as Swainson's Hawk (Buteo swainsonii), Common Nighthawk (Chordeiles minor), Chimney Swift (Chaetura pelagica) and Barn Swallow (Hirundo rustica) migrate south of the equator to take advantage of flushes of insects, while wintering Eastern Kingbirds (Tyrannus tyrannus) are frugivorous in South America. Movements of some of these species do not appear to include long stops or timing that would match peak NDVI values (Brown & Brown, 1999; Bechard et al., 2010; Brigham et al., 2011), and for other species, data are inadequate to assess timing (Murphy, 1996; Cink & Collins, 2002). The matching of Bobolink movements to the primary productivity of natural grasslands, and the lack of matching to agricultural land primary productivity, suggests that the historical distribution and the seasonal phenology of grasslands have served as an ultimate cue to shape the species' non-breeding distribution in both time and space. In Venezuela, Bobolinks co-occur with Dickcissel (Spiza americana), another grassland-obligate Nearctic–Neotropical migratory bird. The Dickcissel remains in Venezuela throughout the austral summer, exploiting the abundant food supplied by agricultural activities (Basili, 1997). Unlike the Bobolink, it does not undergo a complete pre-alternate moult, likely reducing its nutritional needs.

Conservation Implications

The concentration of the global Bobolink population in time and space during the non-breeding season makes the species vulnerable to environmental stochasticity and localized threats. For example, diminished food resources from climate change or direct habitat loss during the non-breeding period could reduce individual survival. Bobolinks are subjected to control measures, some of which are lethal, to reduce crop seed depredation (López-Lanús et al., 2007; Renfrew & Saavedra, 2007; Blanco & López-Lanús, 2008). In addition, the spatio-temporal concentration of Bobolinks allows for efficient trapping for the pet trade industry (Di Giacomo et al., 2008).

The most significant currently known anthropogenic threat occurs in Venezuela and Bolivia, where monocrotophos, an organophosphate insecticide that is highly toxic to birds (Parsons et al., 2010), is commonly and frequently applied to rice as a fungicide and insecticide (Renfrew & Saavedra,

2007; Pieters *et al.* 2011). Basili (1997) documented intentional poisoning of Dickcissel and Bobolink flocks with this pesticide in northern Venezuela, documented as a crucial staging area for the global Bobolink population in this study.

Conversion of forest and grasslands to mechanized agricultural crop production in Bobolink staging and wintering areas has exacerbated agriculture-related threats to Bobolinks. In Venezuela, the area planted to rice increased from 38,000 ha in 1951 to 238,600 ha in 2010 (628%; IRRI, 2012). Conflicts with Dickcissels as pests in rice and sorghum in Guarico State, the core of the Bobolink staging area in this study, is well documented (Basili and Temple 1999). In Bolivia, Bobolinks stopped or wintered in or adjacent to the Department of Santa Cruz, and large flocks have been repeatedly documented in this region throughout the winter (Renfrew & Saavedra, 2007). In this department, where over half of the country's rice is produced (FAOSTAT, 2012), *c.* 260,000 ha undergo land use changes annually, mostly via deforestation; 41% of forests have been converted to crops (Killeen *et al.*, 2008). Simultaneously, native grasslands in part of the Bobolink's Argentinean range have been replaced by development and agriculture (Krapovickas & Di Giacomo, 1998), including for the expansion of rice production (Blanco *et al.*, 2006).

Spatial data from emerging technologies such as light-level geolocators are providing a quantum leap forward towards a better understanding of potential and actual threats posed to migratory birds, as well as migratory connectivity, general migratory bird ecology, and when during the annual cycle bird populations are limited. Ultimately, effective conservation of migratory birds and other animals will require integrating these data with conservation plans and on-the-ground approaches that consider the entire annual cycle (Marra *et al.*, 2011). Advancing technologies and tools to better track animals over large spatial areas will contribute essential yet thus far elusive data needed to fully understand seasonal movements and the fundamental biology of migratory animals.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Figure S1 Location data from a Bobolink for 2 years.

Figure S2 Early fall migration of four Bobolinks breeding in Oregon.

Figure S3 Spring migratory routes, stopovers, and winter staging areas of four Bobolinks.

Figure S4 NDVI in grassland habitats where Bobolinks winter, showing variation within Bolivia relative to the stability of Venezuela and Argentina.

BIOSKETCH

Rosalind B. Renfrew focuses her research on grassland bird breeding ecology and conservation in agroecosystems and most recently on Bobolink wintering ecology in South America. Her aim is to identify where and how birds are most limited during their life cycle and, in collaboration with partners from across the full range of a species, address the most pressing threats to populations.

Author contributions: R.B.R. conceived and coordinated the research, analysed the data and led the writing; N.P and D.K. collected the data and provided feedback and interpretation; J.F. provided technical support and interpretation; J.S. analysed NVDI data and provided interpretation; and P.P.M. conceived research, provided conceptual interpretation and assisted in the writing.

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