IMPROVING THE EFFECTIVENESS OF LAND SHARING CONSERVATION EFFORTS

FOR NORTH AMERICAN GRASSLAND BIRDS

By

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ABSTRACT OF THE DISSERTATION

Improving the effectiveness of land sharing conservation efforts for North American

grassland birds

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Grassland birds are experiencing persistent population declines in North America and elsewhere. Protected grasslands are rare, and private grasslands are increasingly unsuitable due to intensive agricultural practices. Federal private-lands conservation programs ('land sharing' approaches) are the primary conservation tool, but as populations continue to decline, calls for reform have increased. In this dissertation, I explore ways to improve land sharing conservation efforts for grassland birds at three spatial scales: farm, regional, and continental. First, I evaluate a novel conservation practice within active hayfields designed to increase habitat suitability during the post-harvest period. Next, I develop an empirical social-ecological systems model to evaluate how conservation spending, climate, and farm management interact to influence population fluctuations in a grassland bird species in the Mid-Atlantic U.S. Lastly, I identify regions of increasing agricultural or climate impacts on grassland birds by investigating continental scale changes in the geography of spatial population synchrony. Approaches developed here have global applicability in the effort to conserve biodiversity in the face of expanding agricultural and climatic impacts.

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INTRODUCTION

Agriculture currently occupies ~ 40% of ice-free land on Earth and its expansion and intensification represents one of the greatest threats to biodiversity (Foley et al. 2011, Tilman et al. 2011, Tscharntke et al. 2012). To feed a growing and more affluent human population, agricultural output will likely need to double by 2050 (over 2005 levels), requiring some combination of expansion and intensified management of existing farmland (Green et al. 2005, Tilman et al. 2011). How best to meet this 'yield gap' is one of our greatest challenges, the outcome of which will affect not only human food security, but also the fate of global biodiversity (Tilman et al. 2011, United Nations 2015).

While forests and associated fauna are often displaced by conversion to agriculture, some grassland species, including many birds, can adapt to low intensity uses such as forage crops, pastures, rangelands, and (for some species) even row crops and field margins (Askins et al. 2007). However, management activities and habitat changes associated with intensified production practices often conflict with the needs of these species. This is exemplified by the declines in North American grassland birds and European 'farmland' birds (a group that includes many grassland specialists) of ~ 50-60% since the 1960s (Gregory and Burfield 2018). Agricultural intensification has been implicated as a primary cause (Donald et al. 2001, Peterjohn 2003). Solutions are needed within grassland biomes and other agriculturalized landscapes to help stem ongoing population declines not just in North America and Europe (Figure 1), but elsewhere around the globe as well (Attwood et al. 2009, Azpiroz et al. 2012).

Globally, grassland and savanna ecoregions occupy about a quarter of all land area and bear a disproportionate share of the global agricultural burden (~70% and 50% of area in agricultural production, respectively; Ramankutty et al. 2008). Grasslands in temperate regions have been especially hard hit, with all six major biomes currently ~71-

83% in agricultural production (Table 1). Such extensive agricultural activity is due in part to flat topography, fertile soils, and lack of trees, all of which are conducive to farming. This 'agricultural opportunity cost' (i.e., high land values; Venter et al. 2014) contributes to the status of temperate grasslands as one of the least protected biomes on earth with only 5% under some form of conservation protection (Hoekstra et al. 2005). Expansion of this protected area network is likely to face even more obstacles in a future with double the agricultural production demands.

Even if land protection efforts in temperate grasslands can achieve the U.N. Convention on Biodiversity target of 17% protected, this strategy alone is likely to be inadequate for many species. In highly productive agricultural regions, reserves large enough to accommodate sustainable populations of wide-ranging, nomadic, or thinly distributed species (e.g., ungulates, prairie grouse) are likely to be rare (Mallon and Zhigang 2009). And even for smaller less-mobile species the surrounding matrix can act as a drain on regional populations if it is attractive habitat but does not permit adequate reproductive success (Seigel and Lockwood 2010). That birds are actively using this agricultural matrix is evidenced by the fact that in North America, greater than 80% of grassland bird populations currently occur on private lands, with closer to 95% in some states (Stauffer et al. 2017, Zuckerberg et al. 2018). In some instances, endangered grassland species have even become dependent on agricultural land uses that mimic natural disturbances which are now rare (e.g., the Sociable Lapwing, *Vanellus gregarious*, in Eurasia, and the Mountain Plover, *Charadrius montanus*, in the North American Great Plains; Kamp et al. 2011, Dreitz and Knopf 2007). Together, these factors point to the importance of developing effective 'land sharing' conservation strategies in grasslands – those that make working lands more amenable to wildlife – as a needed complement to grassland reserve creation efforts ('land sparing'; Phalan et al. 2011).

In this dissertation, I explore approaches to improve land sharing conservation for North American grassland birds at three different spatial scales: farm, regional, and continental. As agriculture and grassland fauna share many commonalities throughout the temperate world, the insights and models developed here also have the potential for global application. The dissertation is organized into three chapters which I introduce in the sections that follow.

Evaluation of unharvested refugia for grassland bird conservation within active hayfields

Hayfields consist of grasses and other vegetation grown to harvest and store for winter livestock food. They make up a large fraction of grassland bird habitat in many regions of North America and elsewhere, and harvest timing generally coincides with bird nesting with negative consequences for reproduction (Nocera et al. 2005, Grüebler et al. 2015). Hay harvesting not only destroys nearly all active nests, but also causes drastic changes to the habitat, removing all biomass higher than ~10 cm. Re-nesting occurs in some species if there is enough time left in the season and the inter-harvest timing is adequate (~65 days; Perlut et al. 2006). However, other species such as the Bobolink (*Dolichonyx oryzivorus*) are reluctant to re-nest and often abandon a field and leave the area immediately following a harvest (e.g., Owens and Myres 1973, Perlut et al. 2006, Grüebler et al. 2015). If farmers could be compensated for adjusting their harvesting practices to make the post-harvest habitat more desirable, then field abandonment might be lessened and overall reproductive success improved. This chapter describes a field evaluation of a novel grassland bird conservation measure within active hayfields: intentionally leaving un-harvested portions within the field to discourage field abandonment and promote re-nesting. The focal species in the analysis

are Bobolink, Grasshopper Sparrow (*Ammodramus savannarum*), and Eastern Meadowlark (*Sturnella magna*). Results demonstrate the effectiveness of a partial-field approach to in-field conservation efforts in working hayfields and can inform broader efforts to conserve grassland birds and other species in agricultural ecosystems.

This chapter was formatted for *Avian Conservation and Ecology,* and was accepted for publication there: Allen, M. C., Burger, J., Lockwood, J. L. (*in press*). Evaluation of unharvested refugia for grassland bird conservation within active hayfields. Avian Conservation and Ecology.

Climate-driven variation in farm management explains population fluctuations in a grassland songbird: an integrated social-ecological model

Is federal spending to improve habitat for grassland birds on farms effective in the sense that it is having a measurable influence on their populations? Large federal programs exist in the U.S. and Europe that pay farmers to alter their practices (e.g., rest fields, delay harvests) in ways that benefit birds and other organisms (Kleijn et al. 2011, USDA ERS 2018). There is a growing call from scientists on both continents to rigorously evaluate outcomes of these programs (and increase effectiveness) at a regional scale, in part because populations of grassland birds (and farmland birds generally) continue to decline (Purvis et al. 2009, Pe'er et al. 2014, Briske et al. 2017). There is also an increasing realization in conservation and applied ecology that such efforts should be viewed not just as simple cause-and-effect, but as a thread within a larger social-ecological system of causes and effects; spending is one of many climatic, economic, social, and ecological drivers of farmer management behavior, which in turn is one of many influences on bird populations (Malawska et al. 2014). In this chapter, I

examine how conservation spending, climate, and farm management interact to influence population fluctuations in the Grasshopper Sparrow, a declining grassland bird that, in the eastern United States, is dependent on agricultural grasslands. To this end, I build an empirical social-ecological systems model using the statistical technique of latent-variable structural equation modelling and public time series data from the Mid-Atlantic U.S. Results can serve as a model for the empirical evaluation of conservation efforts at a regional scale within a social-ecological systems context.

This chapter is formatted for *Journal of Applied Ecology* and will be submitted there (Allen, Lockwood, & Burger, *in prep.*).

Shifting geographies of spatial synchrony in North American grassland birds: a window into regional population drivers and vulnerabilities

The North American prairie is one of the most human-altered ecosystems on Earth with severe consequences for the continent's grassland bird populations (Sampson and Knopf 1994). Expansion of agricultural grasslands elsewhere in North America via land clearing created new habitats for grassland birds, but intensification of management in the decades following World War II have led to large-scale population declines and the question of whether working agricultural landscapes are still capable of supporting viable grassland bird populations (Peterjohn 2003, Askins et al. 2007; Figure 1). At the same time, it is increasingly apparent that grassland bird populations of many species are highly susceptible to climate, particularly heat and drought, raising serious concerns about their future in a warming world (Gorzo et al. 2016, Wilson et al. 2018, Zuckerberg et al. 2018). Identifying regions most hard-hit by agricultural intensification

and climate extremes (i.e., where these factors are primary drivers of populations) would be a useful first-step to crafting and implementing effective conservation measures.

This chapter seeks a deeper understanding of North American grassland bird population dynamics and their drivers through the lens of a widespread ecological phenomenon: spatial synchrony. This typically refers to the synchronous fluctuations of spatially separated populations due to exposure to common trophic and environmental conditions and/or connections via dispersal (Liebhold et al. 2004); it can also apply to any time-varying phenomenon that exhibits spatial autocorrelation in its temporal fluctuations (Koenig 2002). Recent studies have shown spatial synchrony to be generally increasing in bird populations of North America, with climate changes implicated as a potential cause (Koenig and Liebhold 2016). Others have pointed out the utility of mapping the intensity of local spatial synchrony (Walter et al. 2017) and of comparing such 'geographies of synchrony' among members of declining guilds to look for common patterns indicative of shared population stressors (Michel et al. 2016). In this chapter, I combine these approaches by examining the geography of decadal changes in spatial synchrony in grassland bird populations across North America. Both climate and farm management activities (which depend on climate) are spatially synchronous phenomena (Paradis et al. 2000, Koenig and Liebhold 2016). If these drivers (or some interaction of the two) have increased their influence on populations in recent decades in a region, then this should be evidenced by a corresponding increase in spatial population synchrony. In this chapter I use data from the North American Breeding Bird Survey (Sauer et al. 2017) to examine and map changes in spatial synchrony of 19 species of grassland bird across North America, highlighting regions of generally increasing or decreasing synchrony to target for further investigation and potential mitigation efforts. More broadly this analysis serves as a model for using changes in the geography of

spatial synchrony as a conservation tool for a declining guild of species where adequate
population data exist.

This chapter is formatted for *Conservation Biology* and will be submitted there
(Allen, Burger & Lockwood, *in prep.*).

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Table 1. Extent of agricultural conversion in the major temperate grassland biomes.

Temperate Grassland Biomes	Area (km^2)[a]	% cropland[b]	% pasture	Total % agricultural
Eurasian Steppe	3.2 M	42	32	74
North American Prairie	2.9 M	48	35	83
'Southern Cone' of South America	1.6 M	19	52	71
Mongolian-Manchurian Grasslands	1.6 M	13	64	77
Southern African Grasslands	1.0 M	11	60	71
Southeast Australian Grasslands	0.3 M	14	60	74

[a]Biome areas calculated using spatial data from Dixon et al. (2014) including grassland habitats in temperate latitudes, and excluding alpine, semidesert, and shrub-steppe.
[b]Agricultural data are % of total biome area calculated using spatial data from 2000 provided by Ramankutty et al. (2008).
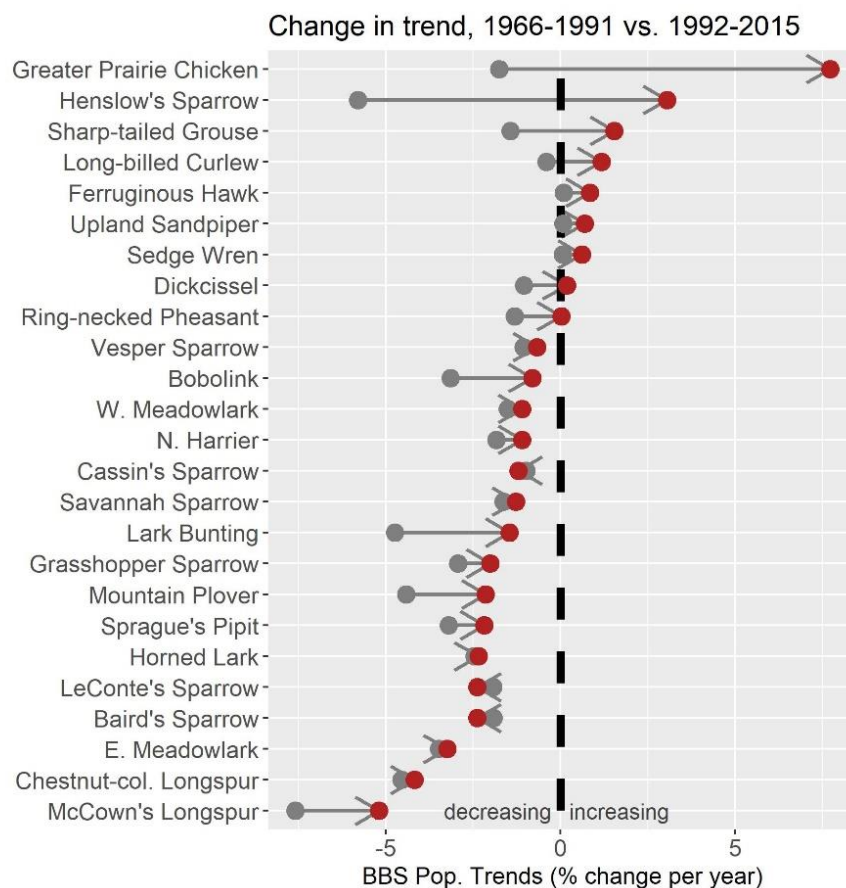
Figure 1. Population trends of 25 North American grassland-obligate bird species. Trend estimates are from the U.S. Geological Survey's North American Breeding Bird Survey (Sauer et al. 2017).

Evaluation of unharvested refugia for grassland bird conservation within active hayfields

ABSTRACT

Agricultural grasslands such as hayfields and pastures frequently act as ecological traps for grassland birds due to harvest practices that interfere with successful nesting. Conservation measures that improve reproductive success while allowing farmers to maintain agricultural outputs are needed to help stem widespread grassland bird population declines. We evaluated leaving uncut patches ('refugia') within harvested hayfields to provide cover, reduce field abandonment, and promote re-nesting by three grassland species: Bobolink (*Dolichonyx oryzivorus*), Grasshopper Sparrow (*Ammodramus savannarum*), and Eastern Meadowlark (*Sturnella magna*). In 2014-2016, we left five refugia (0.25 ha each, shapes varying from square to linear) within a 23-ha hayfield in New Jersey, USA. We found refugia were used more relative to cut areas by Bobolink and Grasshopper Sparrow, but not by Eastern Meadowlark, possibly due to different foraging preferences among species. The presence of refugia appears to have reduced field abandonment following harvest in all three years for Bobolink and Grasshopper Sparrow, but not Eastern Meadowlark, when compared to two adjacent fields that lacked refugia. We observed territorial singing, but no evidence of re-nesting in refugia following harvest, though this may relate to the relatively late harvest dates (26 Jun-3 Aug). Response patterns were consistent over the three years of the study and suggest that leaving small refugia within active hayfields could be a valuable supplement to current management incentive approaches.

INTRODUCTION

Grassland birds around the world are increasingly reliant on agricultural and other anthropogenic land uses (e.g., airports, landfills), where their population dynamics are tightly linked to management practices and economic concerns (Askins et al. 2007, Batáry et al. 2015, Dotta et al. 2016). Globally, over 70% of the land area in grassland biomes have been converted to agricultural uses, and the fraction is even higher (~83%) in North America where hay, pasture, and fallow fields now represent the dominant source of grassland bird habitat (Askins et al. 2007, Ramankutty et al. 2008, Dixon et al. 2014). In the first half of the 20th century, North America's agricultural landscapes supported thriving grassland bird populations, but subsequent trends toward production intensification and conversion to row crops have contributed to widespread population declines, raising the question of whether viable grassland bird populations are compatible with modern agriculture (Peterjohn 2003, Askins et al. 2007). At the same time, conservation opportunities exist where grassland habitat is created and maintained as a byproduct of economic activity (e.g., hay production, airport maintenance), leading to more total grassland in some regions than was historically present (e.g., the northeastern United States; Peterjohn 2003). With appropriate management, anthropogenic grasslands can be assets rather than liabilities for grassland bird populations (Bollinger et al. 1990, Perlut et al. 2008).

In northeastern North America, grassland birds normally arrive on the breeding grounds from mid-April to mid-May, and are actively nesting through June–August, depending on the species (Perlut et al. 2006, Jaster et al. 2012). Hayfields make up a large fraction of grasslands available to these species in Northeast and Mid-Atlantic states: an estimated 2.2 M ha in 13 states (U.S. Fish and Wildlife Region 5) in 2012, compared to 2.5 M ha of pastureland and <0.3 M ha of airport grasslands (Devault et al.

2012, USDA 2012). Hay harvest typically occurs in June, the middle of the breeding season for most grassland birds and destroys nearly all nests active at the time of harvest (Bollinger et al. 1990, Luscier and Thompson 2009). Earlier and more frequent hay harvests over the past half-century are implicated in population declines of grassland bird species in the northeast (Bollinger et al. 1990, Troy et al. 2005, Perlut et al. 2008), and while re-nesting after harvest can occur, structural alteration and reduction in food resources cause some species to largely abandon fields or forego re-nesting opportunities for the season (Perlut et al. 2006, Luscier and Thompson 2009, Grüebler et al. 2015).

Conservation measures for grassland birds in hayfields have primarily focused on monetary compensation for farmers by federal, state, and non-governmental groups to delay harvests and allow time for grassland birds to rear their broods, but funding limits these practices to a relatively small area in most eastern states (Troy et al. 2005; MCA, unpubl. data). For example, Troy et al. (2005) report that <1,500 ha were enrolled in such programs in Vermont in 2003, or less than 1% of total hayfield area in that state (USDA 2012). Both lack of funding and a lack of adoption by farmers likely contribute to the limited scope of the programs. Delaying harvest interferes with normal hay production as hay quality declines later in the season, leading to an inferior agricultural product (Nocera et al. 2005, Troy et al. 2005). A broader suite of practical, cost-effective conservation management measures would be useful for enhancing suitability of agricultural grassland habitats for birds, while maintaining the farm's economic sustainability and agricultural production levels. If farmers can maintain profits and receive additional payment incentives while still providing a benefit to birds, more farmers may adopt such practices.

Within-field conservation approaches for grasslands (i.e., interventions embedded within active agricultural fields) have gained traction recently, mainly in Europe, and especially for invertebrates (Buri et al. 2013, 2014, Garibaldi et al. 2014) and birds. For birds, these have included 1) finding individual nests and protecting them through agreements with farmers to avoid harming them with machinery (Koks and Visser 2002, Kragten et al. 2008, Grüebler et al. 2012), and 2) leaving patches or strips of standing crop to provide food and shelter for birds for the remainder of the season (Broyer 2003). The benefits of the former method, while labor intensive, are established (Musters et al. 2001), while the benefits of the latter are unknown for most species (but see Broyer 2003, Masse et al. 2008). As some species are known to abandon fields and delay or avoid re-nesting following harvest (Owens and Myres 1973, Perlut et al. 2006, Grüebler et al. 2015), it is especially relevant whether uncut refugia can provide enough food and cover for birds to remain on fields to re-nest and thus improve reproductive success. Delaying harvest in small patches or strips within hayfields is less expensive than entire fields, and thus the former has the potential to act as a lower-cost, more-widespread supplement to the existing landscape of hayfield conservation incentive programs.

The goal of this study was to evaluate the utility of leaving uncut refugia in hayfields (Fig. 1) for promoting site persistence of three grassland bird species in eastern North America: Bobolink (Dolichonyx oryzivorus), Grasshopper Sparrow (Ammodramus savannarum), and Eastern Meadowlark (Sturnella magna). Specific objectives were to 1) compare bird use of refugia and harvested reference areas before and after harvest, and 2) evaluate the role of refugia in promoting site persistence and re-nesting following harvest. We hypothesized that some or all of these species would show greater use of refugia areas after the harvest and would also show lower rates of

abandonment (i.e., maintain higher densities) in the field with refugia compared with completely-harvested fields.

METHODS

Our study consisted of collecting data in three adjacent hayfields: a 'primary' field in which we left rectangular unharvested areas, and two completely-harvested nearby fields (named 'north' and 'south') used for comparison (Fig. 2).We performed four primary analyses: 1) a before-after-control-impact paired series (BACIPS; Conner et al. 2016) comparison of bird abundance in the rectangular unharvested patches ('refugia') and paired harvested ('reference') areas pre- and post-harvest, 2) a post-harvest evaluation of refugia usage, evaluating the effects of shape and time since harvest, 3) a comparison of field abandonment after harvest in the refugia-containing field with the two completely-harvested fields, and 4) an analysis of the spatial and temporal pattern of nest initiations in relation to refugia location and harvest timing. These analyses are described in detail below.

Study area

The study took place May–August 2014–2016 in Hunterdon County, New Jersey, USA. This urbanizing agricultural region lies 30 miles west of New York City and is in the Piedmont physiographic province characterized by low, rolling topography. Land use is dominated by forest (42%), agriculture (28%), and developed land (25%), while dominant field crops include hay (61%), corn (21%), and soybeans (12%; USDA 2012, NJDEP 2015). The three hayfields studied were referred to as: primary (23 ha; 40°34′26″N, 74°45′47″W), north (13 ha; 40°34′37″N, 74°45′36″W), and south (8 ha;

40°34′12″N, 74°45′36″W). The fields were adjacent (separated by tree lines; Fig. 2) and all contained a similar mix of fescue (*Schedonorus* sp.), orchard grass (*Dactylis glomerata*), little bluestem (*Schizachyrium scoparium*), vetch (*Vicia* sp.), and other less common species. Bobolink, Grasshopper Sparrow, and Eastern Meadowlark were the only grassland-obligate bird species nesting in the fields.

Bird use of refugia

We evaluated bird use in refugia and in paired reference areas before and after harvest using a BACIPS design (see Fig. 2). This experiment took place only in the primary field. The BACIPS design allowed us to measure treatment effects while controlling for local variation within the field (Conner et al. 2016). Five rectangular 0.25-ha refugia were designed in a geographic information system (GIS) ranging from square (50 x 50 m) to increasingly narrow and elongated (41 x 61 m, 33 x 77 m, 24 x 105 m, and 15 x 167 m). Refugia area totalled 1.25 ha or 5% of the field. We sited refugia using a 200 x 200 m grid overlaid on the field with a transect line bisecting each cell (Fig. 2). We randomly assigned refugia to a transect and positioned it along the line to allow identical coverage with a paired reference area. Refugia boundaries were marked in the field immediately prior to harvest using a handheld GPSMap 62s global positioning system (GPS; Garmin International, Olathe, Kansas, USA) and pink flagging. The farmer could mow around most corners and edges of the refugia with the large hay mower, but some corners and berm areas were 'cleaned up' after the harvest with a smaller rotary mower adjusted to approximately the same height (~12 cm). We used the same refugia locations in all three years. The farmers determined the harvest dates each year based on weather and other factors. The primary field was harvested 26 June 2014, 31 July–3 August 2015, and 5–6 July 2016. Refugia were mowed off between breeding seasons (Sep–Mar).

One observer (MCA) completed bird surveys along the transects twice per week, between 13 ± 11 (SD) and 149 ± 26 min after sunrise, from 15 May until early- to mid-August 2014–2016. The order and direction of surveys was alternated each time. The observer walked slowly (19 ± 3 m/s SD), recording the following about each bird or group of birds to allow mapping and density calculations: species, number of individuals, GPS-derived Universal Transverse Mercator coordinates of the observer (accuracy ~3–5 m), distance using a laser rangefinder (accuracy ± ~0.5 m), and compass bearing, adjusted for magnetic declination. We calculated densities within refugia and reference areas as the number of individuals per 0.25-ha rectangle per survey based on mapped locations in a GIS. We excluded individuals classified as 'fly-overs' or juveniles from analyses and lumped individuals of both sexes as they were not always possible to distinguish (e.g., by late July, many male Bobolinks have molted into female-like plumage).

Imperfect detection could bias our results, especially if detection probability for a species changes in refugia and reference areas unequally following the harvest. For example, if relative detectability decreases in cut areas (e.g., due to behavioral differences) then refugia preference could be over-estimated; if, however, lack of vegetation makes it easier to see birds then not accounting for detection probability may have the opposite effect. Distance sampling can correct for these biases, but no individual refugium in our study had the recommended minimum sample size of 60-80 detections to estimate a detection function (Buckland et al. 1993). Pooling among refugia was not possible due to the varying truncation distances required. Therefore, to learn more about potential detection biases, we evaluated changes in detection probability pre- vs. post-harvest in the broader study area; i.e., the primary, north, and south fields. We excluded detections in or behind refugia as these features could cluster birds non-

randomly with respect to transect lines (see Fig. 2). We evaluated detection probability for each species in the R package 'Distance' (Miller et al. 2019) at two truncation distances (40 m, the maximum within-refugium distance, and 100 m) and included group size as a covariate. Sample sizes in all post-harvest groups were still below 60 detections (and mostly < 40, the absolute minimum recommended; Buckland et al. 1993; Table 1). We therefore evaluated nine models (all combinations of key functions and adjustment series in Miller et al. 2019) with no pre/post-harvest covariate for most species and distance ranges. The exceptions were Grasshopper Sparrow and Eastern Meadowlark (truncation distance of 100 m) both of which had 53-59 detections. For these groups we evaluated six additional models (based on the half-normal and hazard-rate models) with a covariate indicating pre- vs. post-harvest. For all groups, we selected a top model based on AIC and evaluated the top model based on the Cramer-von Mises goodness-of-fit test (alpha = 0.05) as well as effect sizes and standard errors. Finding relatively high detection probabilities (0.79–1.00) at 0–40 m and a lack of evidence that the hay harvest has a large effect on distance-based detectability (see Results, Table 1), we opted not to adjust densities for detection probability prior to statistical analysis of refugia usage.

The difference in density estimates between paired refugia and reference areas during each survey served as the dependent variable in our analysis (Conner et al. 2016). These data were calculated from a subset of the biweekly survey data centered on the harvest date for each year: 12 weeks of data (i.e., 12 pre- and 12 post-harvest surveys) in 2014 and 2016, and six weeks of data (6 pre- and 6 post-harvest surveys) in 2015 due to a later harvest (31 Jul–3 Aug). We used repeated-measures linear mixed models to test for the fixed effects of year and time period (pre- or post-harvest), and a random effect of transect (R package 'lme4'; Bates et al. 2015). We then ran identical

models on refugia and reference area densities separately to determine if differences observed were due to a change in abundance within refugia, reference areas, or both. Effect sizes were evaluated based on fixed-effect coefficients with bootstrapped 95% confidence intervals (10000 iterations), as well as conditional F-tests with Kenward-Roger-corrected degrees-of-freedom (Bates et al. 2015). An alpha level of 0.05 was used for all tests.

Refugia post-harvest dynamics

In 2014 and 2016, which both had six weeks of post-harvest transect bird surveys, we investigated if there was an increase or attenuation of refugia usage with time following the harvest, as well as if the magnitude of post-harvest usage varied based on patch shape. We used general linear models (function 'lm'; R Core Team 2017) with the dependent variable being the difference between paired refugia and reference areas at each transect averaged by week during the post-harvest period. Independent variables were 1) days since harvest, 2) length:width ratio of refugia, and 3) year (2014 or 2016).

Post-harvest field abandonment

To examine post-harvest field abandonment, we performed transect bird surveys in the two completely-harvested adjacent fields ('north' and 'south' fields; Fig. 2) with the same time schedule and protocol as in the primary field. The north field was harvested 16 July 2014, 31 July 2015, and planted to row crops in 2016. The south field was harvested 21 July 2014, 6 August 2015, and 24–27 July 2016. If refugia served to prevent abandonment, we expected to see greater reductions in field-level densities after harvest in the fields lacking refugia. We established two 200-m transects in each

field, positioned to provide maximum coverage: 77% of the north field and 100% of the south field were within 100 m of the transect lines.

We calculated field-level density as the average number of individuals observed per hectare of grassland within 100 m perpendicular to the transect line during each survey. As above, we excluded juveniles and fly-overs and lumped both sexes together for this analysis. We corrected for imperfect detection by dividing densities by species-specific detection probabilities derived from the distance sampling analyses discussed above (100 m truncation distance; Table 1).

Nesting phenology and harvest impact on nests

We searched for nests in the primary (2014–2016) and north (2014–2015) fields during daylight hours, usually 0500–0900 h and 1500–1900 h (EST) to reduce heat stress on eggs or young. We walked parallel transects through the field at a spacing of 10 m apart weekly from 15 May to 22–23 July, guided by a GPS, and agitating vegetation with a 2-m stick to locate nests by flushing incubating females (Winter et al. 2003). The search path was shifted by 5 m in alternate weeks, with the effect of covering the entire area at 5-m spacing in each two-week period. We also looked for food-carrying behavior of adults and found nests by watching as they fed nestlings (this was also done during transect abundance surveys which extended into early- to mid-Aug). We obtained GPS coordinates of nests and checked them every 1–3 d to determine contents, stage, and outcome.

We classified nests as either 1) inside or outside of refugia in a GIS, and 2) initiated pre- or post-harvest based on phenology. We estimated the date of initiation (first day of incubation) for each nest by back-dating from the estimated hatch date or forward-dating for nests found during egg laying (assuming one egg laid per day). This

date was then used to estimate a first egg date and a projected fledge date for each

nest. We assumed incubation and nestling periods of 12 and 10 d for Bobolink, 12 and 9

d for Grasshopper Sparrow, and 13 and 11 d for Eastern Meadowlark (Vickery 1996,

Jaster et al. 2012, Renfrew et al. 2015).

RESULTS

Bird use of refugia

Detection probabilities were 0.79–1.00 for all species at 0-40 m and were 0.48–

0.77 at 100 m (Table 1). We found little evidence of a consistent effect of hay harvesting

on detectability. For Grasshopper Sparrow (0–100 m), the top model included the

harvest covariate (scaling coefficient: -0.338 [0.168 SE]; top model without covariate:

ΔAIC = 2.10). Models predicted higher detectability in harvested than unharvested fields

(0.62 [0.07] vs. 0.52 [0.04]). As an illustration, applying these detection probabilities to a

count of 4 individuals would yield corrected estimates of 7.7 and 6.5, respectively. The

best-performing model for Eastern Meadowlark (0–100 m) lacked a harvest covariate,

though it ranked not far above the top model that contained a covariate (ΔAIC = 1.50).

This model predicted a trend of higher detection probability in unharvested grass (0.81

[0.09] vs. 0.69 [0.08]), though the standard error for the scale coefficient was high (0.310

[0.350]; C.V. = 94%).

The relative use of refugia (i.e., density in refugia minus reference areas)

increased from pre- to post-harvest for Bobolink (3-yr mean: 0.09 to 1.38 individuals

refugium^{-1} survey^{-1}) and Grasshopper Sparrow (0.07 to 0.81), but not for Eastern

Meadowlark (0.00 to 0.02; Table 2, Fig. 3). Supporting these patterns, confidence

intervals of 'time period' coefficient estimates from mixed effect models did not overlap zero for Bobolink (βpre vs. post = -1.45 [95% C.I. = -2.35, -0.52]) or Grasshopper Sparrow, β = -0.68 [-0.87, -0.50]), but widely overlapped zero for Eastern Meadowlark (β = 0.03 [-0.12, 0.17]; Table 3). Relative use of refugia also varied by year for Grasshopper Sparrow, with lower values in 2014 compared with 2015 and 2016 (Table 3, Fig. 3).

For Bobolinks, the difference in abundance between refugia and reference areas was driven by reduced densities in reference areas post-harvest (3-yr mean: 97% decrease; mixed effect model, βpre vs. post = 0.64 [0.32, 0.97]; Tables 2 and 3), and less so by increased densities in refugia (114% increase; β = -0.81 [-1.69, 0.08]). Grasshopper Sparrow density both decreased in reference areas (65% decrease; β = 0.13 [0.04, 0.21]), and increased in refugia post-harvest (243% increase; β = -0.55 [-0.71, -0.39]). Eastern Meadowlark density remained at similar levels in both reference areas (β = -0.07 [-0.17, 0.04]) and refugia (β = -0.04 [-0.15, 0.07]) following the harvests.

Refugia post-harvest dynamics

Greater length to width ratios were associated with higher relative Grasshopper Sparrow densities in refugia (general linear model, β = 0.09 [95% C.I.: 0.05, 0.13]; $F_{1,56}$ = 18.8, $P < 0.001$), but this factor was not predictive for any other species ($F_{1,56}$ = 0.03–0.11, P = 0.74–0.87). The difference between refugia and reference areas increased for Eastern Meadowlark with days after harvest (β = 0.010 [0.001, 0.018]; $F_{1,56}$ = 4.5, P = 0.04), while Bobolink and Grasshopper Sparrow showed no change ($F_{1,56}$ = 0.3–0.9, P = 0.34–0.60). Grasshopper Sparrow usage varied by year, with higher relative densities in refugia post-harvest in 2016 (βvs. 2014 = 0.61 [0.30, 0.92]; $F_{1,56}$ = 15.5, $P < 0.001$).

Post-harvest field abandonment

Field-level densities of Bobolink on the two completely-mowed fields averaged 1.1 individuals/ha (3-yr mean) before the harvest, dropping to zero afterwards (100% decline in all years); Grasshopper Sparrow densities dropped an average of 83%; Eastern Meadowlark dropped an average of 14% and showed less consistency among fields and years (Table 4). In the primary field which contained refugia, Bobolink densities dropped less steeply in all three years following harvest, by an average of 57% (1.2 to 0.8/ha), while Grasshopper Sparrow and Eastern Meadowlark densities both increased in all three years (Table 4).

Nesting phenology and harvest impact on nests

We found a total of 26 nests of target species: 17 Bobolink (12 in primary, 5 in north/south fields), 6 Grasshopper Sparrow (2 in primary, 4 in north/south), and 3 Eastern Meadowlark (2 in primary, 1 in north/south). Prior to hay harvest, 13 nests fledged and 9 failed (Bobolink: 6 fail, 9 fledge; Grasshopper Sparrow: 2 fail, 3 fledge; Eastern Meadowlark: 1 fail, 1 fledge). Of the four nests still active during hay harvest events, three nests (two Bobolink and one Grasshopper Sparrow nests) were destroyed by hay machinery, whereas the only nest still active in a refugium (one Eastern Meadowlark nest) was spared and fledged young. No re-nesting was observed post-harvest, but multiple Grasshopper Sparrow males were observed singing within the refugia. Based on estimated initiation dates and nest cycle lengths, 50% of the 26 nests monitored either fledged or would have fledged by 24 June, and 95% by 23 July. For Bobolink, the only species with adequate sample sizes, these dates were 21 June and 12 July.

DISCUSSION

We found increased use of refugia by Bobolinks and Grasshopper Sparrows relative to reference areas following the hay harvest (Fig. 3), suggesting that refugia are likely of value to these species. Refugia may have reduced field abandonment as both Bobolinks and Grasshopper Sparrows decreased sharply following harvest in the completely-harvested fields, but less steeply or not at all in the primary field with refugia. In contrast, Eastern Meadowlarks did not show a change in relative use of refugia areas pre- vs. post-harvest, and experienced a lower magnitude and consistency of field abandonment following harvest in the fields that lacked refugia; however, this species did increase its relative use of refugia somewhat in the weeks following harvest. We observed no evidence of re-nesting in the refugia other than territorial singing by Grasshopper Sparrows, perhaps because hay harvests occurred relatively late in the breeding season (26 Jun–3 Aug).

Incentivized conservation management measures such as leaving unharvested refugia can be considered a "land sharing" approach in which agricultural production and biodiversity conservation coexist (Dotta et al. 2016). In other words, it is a method of reducing competing claims (economic vs. conservation) for grasslands to the benefit of both birds and farmers. Grassland birds may be particularly suited to such an approach in the northeastern U.S. as the alternative ("land sparing" or the creation of grassland protected areas) requires costly management to maintain habitats and could potentially shift intensive grassland agriculture elsewhere on the landscape with these fields continuing to function as ecological traps (Perlut et al. 2008, Seigel and Lockwood 2010). The cost of maintaining such grassland preserves may partly explain the disproportionately low representation of grassland birds in protected area networks of the northeastern U.S. (Stauffer et al. 2017). In Europe and increasingly elsewhere,

comprehensive agri-environmental approaches integrating biodiversity into agricultural landscapes using a toolbox of species- or guild-specific conservation measures are gaining popularity (Perlut et al. 2011, Batáry et al. 2015). Our results suggest that such an approach in the U.S., and in particular in the northeast, may provide real conservation benefits to grassland birds.

We suggest that leaving refugia within active hayfields is a tool that could be used in concert with a suite of other management tactics for grassland birds in working landscapes such as row crop-to-grass conversion and whole-field delayed harvest programs (e.g., the Conservation Reserve Program [CRP]; Nocera et al. 2005, Troy et al. 2005). While the population-level effects (i.e., increased carrying capacity and fecundity) may be less than with existing CRP-like programs, the economics of leaving refugia gives it the potential to affect a larger number of fields. Refugia in our study occupied only 5% of the field area and would therefore require compensation for a ~5% loss in revenue of first-cutting hay. Refugia – ideally centrally-located (Renfrew et al. 2005) – could then be harvested as part of a second cutting after the grassland bird nesting season. The low cost of implementation and flexibility for both conservation professionals and farmers may make it a viable option, especially where other approaches are not feasible.

Bird use of refugia

Our finding that Bobolink and Grasshopper Sparrow were more abundant in refugia vs. reference areas after harvest is encouraging as it shows that even small (0.25 ha) areas of longer grass can provide attractive habitat for these species compared with relatively bare cut areas. These results agree with a similar study in French hayfields that found Corn Crake (Crex crex) and Quail (Coturnix coturnix)

densities increased ~2–6 fold inside 10-m-wide uncut strips following harvest and documented several grassland Passerines using the strips (Broyer 2003). Bobolink and Grasshopper Sparrow primarily eat seeds and foliar invertebrates (Vickery 1996, Renfrew et al. 2015), and thus the refugia in our study likely maintained foraging conditions at least at a minimum level required by those species. Seed availability and foliar, though not necessarily soil-dwelling, invertebrates have been shown to be lower in hayfields following harvests (Vickery et al. 2002, Zalik and Strong 2008). A discrepancy in the effects of mowing on above- and below-ground invertebrates may have contributed to our finding that Eastern Meadowlark was not attracted to refugia but instead foraged in cut and uncut areas at about equal shares. This species generally feeds on invertebrates at or below the soil surface (Jaster et al. 2012), and other soil-probing species (e.g., European Starling [*Sturnus vulgaris*]) actively avoid taller vegetation due to poor visibility of predators and prey items (Devereux et al. 2004). We observed both Bobolink and Grasshopper Sparrow feeding on seed heads in refugia (e.g., thistle [*Cirsium arvense*], foxtail [*Setaria spp.*]) that were absent in cut areas, as well as on Orthopterans and various caterpillar-like larvae. Eastern Meadowlarks were most commonly observed foraging on the ground, frequently in cut areas with short vegetation, but no prey items were identified.

Refugia post-harvest dynamics

We hypothesized that the attractiveness of refugia to grassland birds might change with time following the harvest as the surrounding matrix regrew and/or the refugia were depleted of resources. However, Grasshopper Sparrow and Bobolink showed no change in their relative use with time post-harvest. Eastern Meadowlarks increased their relative use of refugia over time, but the magnitude of the increase was relatively small: a slope of 0.01, or a total change of ~0.4 individuals refugium^{-1} survey^{-1}

over the 6-week post-harvest period. The reason for this change is unclear but could be due to seasonal shifts in diet or prey availability.

Grasshopper Sparrow relative density in refugia increased along a gradient of short and compact to long and narrow (i.e., low to high length:width ratios); however, Bobolink relative density did not. This may be explained by differences in territorial behavior between the species in the latter part of the breeding season. Longer features could theoretically accommodate more territorial individuals than more-compact ones as strip-like refugia can potentially stretch across multiple territories. Grasshopper Sparrows are multiple-brooded with a ~90-d breeding season extending into August, and so may have remained territorial during the late-season post-harvest period of our study (Vickery 1996). In contrast, Bobolinks are typically single-brooded and start to form loose post-breeding flocks by early- to mid-July (Renfrew et al. 2015; MCA, unpubl. data). Our observations support this potential difference in territorial behavior between Grasshopper Sparrows and Bobolink late in the season, as 20% of the male Grasshopper Sparrows we observed were still singing in August, whereas no male Bobolinks were singing at this time.

Post-harvest field abandonment

The fact that our primary field containing refugia maintained a population (albeit reduced) of Bobolinks following harvest, while the two fields that were completely harvested did not in all three years (Table 4), suggests that the refugia promoted site persistence for this species. Hay harvest involves the removal of most plant biomass from the field and consequently represents a dramatic structural alteration and reduction in food for some species. Bobolinks are known to abandon early-mowed hayfields completely following harvest for at least two weeks, presumably due to these alterations

(Bollinger et al. 1990, Perlut et al. 2006). Other grassland species, including Whinchat (*Saxicola rubetra*) in Switzerland, and Baird's Sparrow (*Ammodramus bairdii*) and Sprague's Pipit (*Anthus spragueii*) in the northern Great Plains, experience similarly high rates of field abandonment after hayfield mowing (Owens and Myres 1973, Grüebler et al. 2015). Perhaps most relevant to our study: in Switzerland, increasing the fraction of a hayfield that is left unharvested during the breeding season decreases the proportion of Whinchats abandoning that field (Grüebler et al. 2015).

However, not all species may be as sensitive to habitat changes associated with hay harvesting. Savannah Sparrows (*Passerculus sandwichensis*), for example, largely remained and re-nested in the stubble of cut hayfields in the Champlain Valley (Perlut et al. 2006) and were common on mowed hayfields and edges of cultivated fields in the Great Plains (Owens and Myres 1973). Patterns of field abandonment for Grasshopper Sparrow and Eastern Meadowlark in our study suggest possible intermediate levels of sensitivity. While Grasshopper Sparrow decreased following harvest by an average of 83% in the completely-mowed fields, Eastern Meadowlark only decreased by 14% and showed less consistent patterns among fields and years. Both species increased in abundance in the primary field each year following harvest, possibly due to immigration from harvested adjacent fields. Further study of within-season site fidelity following harvests – i.e., the continuum of 100% remaining to complete abandonment – could lead to further insights on habitat preferences, sensitivity to agricultural practices, and the potential utility of in-field conservation interventions such as refugia.

Nesting phenology and harvest impact on nests

The primary field in our study was harvested relatively late (26 June–3 August vs. the typical May–July; Perlut et al. 2006) due to prioritization of other tasks by the

farmers. This likely led to lower re-nesting rates than would be expected following earlier (May or June) harvests. For example, Bollinger et al. (1990) noted that Bobolinks do not re-nest if failure occurs after 20 June, but they documented re-nesting within unharvested regions of the same hayfields by 5 of 12 pairs that failed due to an earlier-June harvest (sizes of uncut areas not given). Similarly, in Vermont, fields harvested in May were more readily re-colonized by Bobolinks than later-cut fields, an observation that inspired the creation of a novel conservation incentive program (Perlut et al. 2011). This program allows farmers a high-quality hay harvest before 2 June and allows grassland birds time to re-settle and raise a brood before a second harvest is permitted. Grasshopper Sparrow and Eastern Meadowlark have longer nesting seasons, but still are more likely to re-nest following earlier harvests as nest initiations of both species begin to taper off sharply in July (Vickery 1996, Jaster et al. 2012). In general, these factors speak to the importance of further investigations into the utility of refugia in which harvests are carried out earlier in the season when birds may be most likely to use them for re-nesting.

Though refugia within harvested hayfields are isolated habitat islands potentially vulnerable to increased predation, previous studies indicate that nest survival in these areas is not necessarily lower. A study of artificial nests placed in irregularly-shaped uncut patches in Vermont hayfields (mean: 0.3 ha) found only 1 in 29 was depredated (Masse et al. 2008). Whinchat nests in Switzerland spared during the harvest within 10 x 10 m unharvested patches had similar survival to nests in late-harvested fields, and higher survival than those in early-harvested fields (Grüebler et al. 2012). Similar results have been shown for larger non-Passerines, with improved survival of eggs (Musters et al. 2001, Kragten et al. 2008) and precocial young (Broyer 2003) within small unharvested strips or patches, including some protected by temporary electric fencing

(Koks and Visser 2002). Nevertheless, more research into area effects is needed. It is possible that fewer, larger refugia may be preferable to smaller ones for biological as well as practical reasons, including ease of implementation.

Limitations and future research

Our study represents a first look at the benefits of intentionally leaving uncut refugia as a conservation measure for grassland birds in hayfields; however, more research is needed to assess its generality. First, while we demonstrated increased relative abundance in refugia, we did not measure seed and invertebrate resources or quantify foraging behavior. It is possible that some individuals used the refugia to take advantage of perches for singing and predator scanning, though based on the literature and our observations of actively foraging individuals we believe the refugia did provide food as well. Second, due to logistical constraints on the farmer, the harvest date during all three years of our study was later than the regional norm of mid-June (Bollinger et al. 1990, Perlut et al. 2006). Although our results provide information on a stage of the avian life cycle that is under-represented in the literature (Marra et al. 2015), further study in early-harvested fields with refugia is needed to better understand the success of re-nesting attempts of these grassland birds. Finally, though a repeated pattern emerged in all three years, our study was limited in geographic scope. Replication across broader scales is needed to confirm and expand inference to other regions and species. Ideally, these studies would explore more realistic scenarios including non-random siting of refugia that considers the biology of the species (e.g., habitat preferences, edge avoidance), farmers' needs, and prior knowledge of bird use at the site. These considerations would help to maximize conservation benefits while minimizing the economic impact to farmers. We believe that leaving unharvested refugia – essentially a 'partial delayed-mowing' approach – deserves further examination as a potential

supplement to established conservation incentive programs that alter harvest timing.

Such work would have the added benefit of illuminating basic ecological questions such

as differences in habitat preferences and disturbance tolerance among species.

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Tables

Table 1. Distance sampling analysis results for transect bird surveys conducted in three New Jersey hayfields, 2014-2016. Detection probabilities

were estimated for the distance ranges 0-40 m and 0-100 m. The top-performing model (based on Akaike information criterion) is shown for

each species/distance category. We evaluated nine models in each case, except for Grasshopper Sparrow and Eastern Meadowlark (100 m

truncation distance) which had sample sizes adequate to evaluate 6 additional models containing a covariate for pre- vs. post-harvest (see

Methods for details).

Species	Truncation dist. (m)	No. detections (pre- / post-harvest)	Key function	Series	GOF p-value	Covariate	Covariate scale coefficient (SE)	Detection probability (SE)
Grasshopper Sparrow	40	258 (227 / 31)	Half-normal	Cosine	0.60	None	-	0.79 (0.09)
	100	377 (324 / 53)	Half-normal	Cosine	0.36	Pre / Post-harvest	-0.34 (0.17)	Combined: 0.48 (0.02) Stratified (pre): 0.52 (0.04) Stratified (post): 0.62 (0.07)
Bobolink	40	470 (460 / 10)	Uniform	Cosine	0.61	None	-	0.81 (0.06)
	100	763 (734 / 29)	Uniform	Cosine	0.32	None	-	0.59 (0.01)
Eastern Meadowlark	40	74 (40 / 34)	Half-normal	Cosine	0.26	None	-	1.00 (0.11)
	100	144 (85 / 59)	Uniform	Simple Poly.	0.78	None	-	0.77 (0.05)

Table 2. Mean density (individuals / survey) within 0.25-ha refugia and reference areas in a central New Jersey (USA) hayfield before and after harvest. Average density for each of five transects was computed for the pre- and post-harvest periods; these values were then averaged to get the reported means (SE; n = 5).

Species	Year	Refugia		Reference areas	
		Pre-harvest	Post-harvest	Pre-harvest	Post-harvest
Bobolink	2014	0.60 (0.10)	2.12 (0.53)	0.72 (0.13)	0.02 (0.02)
	2015	0.33 (0.11)	0.77 (0.46)	0.10 (0.10)	0.00 (0.00)
	2016	1.03 (0.18)	1.32 (1.06)	0.88 (0.31)	0.03 (0.03)
	mean	0.66	1.40	0.57	0.02
Grasshopper Sparrow	2014	0.08 (0.05)	0.30 (0.13)	0.07 (0.05)	0.02 (0.02)
	2015	0.37 (0.03)	1.33 (0.42)	0.17 (0.11)	0.07 (0.07)
	2016	0.32 (0.09)	1.00 (0.28)	0.33 (0.07)	0.12 (0.08)
	mean	0.26	0.88	0.19	0.07
Eastern Meadowlark	2014	0.03 (0.02)	0.05 (0.03)	0.10 (0.07)	0.17 (0.06)
	2015	0.03 (0.03)	0.30 (0.19)	0.07 (0.07)	0.10 (0.07)
	2016	0.12 (0.07)	0.07 (0.04)	0.02 (0.02)	0.10 (0.10)
	mean	0.06	0.14	0.06	0.12

Table 3. Results of repeated-measures linear mixed models used to examine relative grassland bird use of uncut refugia and harvested reference areas (each 0.25 ha in size) in a New Jersey, USA hayfield, 2014-2016.

Species / Dependent Variable	Independent variables	Coefficient (95% C.I.)	F	df	P
Bobolink / Δ density (refugia–reference)	Intercept	1.72 (0.77, 2.66)			
	Year (2015 vs. 2014)	-0.49 (-1.77, 0.75)	0.3	2 / 292	0.73
	Year (2016 vs. 2014)	-0.28 (-1.28, 0.76)			
	Pre vs. post-harvest	-1.45 (-2.35, -0.52)	9.5	1 / 292	0.002
	Transect (SD, rand. effect)	0.43 (0.00, 1.00)			
Bobolink / Density in refugia	Intercept	1.76 (0.82, 2.70)			
	Year (2015 vs. 2014)	-0.81 (-2.05, 0.43)			
	Year (2016 vs. 2014)	-0.18 (-1.19, 0.82)			
	Pre vs. post-harvest	-0.81 (-1.69, 0.08)	3.1	1 / 292	0.08
	Transect (SD, rand. effect)	0.49 (0.00, 1.09)			
Bobolink / Density in reference	Intercept	0.05 (-0.25, 0.35)			
	Year (2015 vs. 2014)	-0.32 (-0.77, 0.12)	1.7	2 / 292	0.19
	Year (2016 vs. 2014)	0.09 (-0.26, 0.46)			
	Pre vs. post-harvest	0.64 (0.32, 0.97)	14.9	1 / 292	< 0.001
	Transect (SD, rand. effect)	0.00 (0.00, 0.25)			

Table 3. (continued)

Species / Dependent Variable	Independent variables	Coefficient (95% C.I.)	F	df	P
Grasshopper Sparrow / Δ density (refugia–reference)	Intercept	0.49 (0.21, 0.76)			
	Year (2015 vs. 2014)	0.58 (0.33, 0.84)	10.6	2 / 292	< 0.001
	Year (2016 vs. 2014)	0.28 (0.08, 0.49)			
	Pre vs. post-harvest	-0.68 (-0.87, -0.50)	51.7	1 / 292	< 0.001
	Transect (SD, rand. effect)	0.23 (0.00, 0.42)			
Grasshopper Sparrow / Density in refugia	Intercept	0.47 (0.21, 0.72)			
	Year (2015 vs. 2014)	0.66 (0.44, 0.88)	21.7	2 / 292	< 0.001
	Year (2016 vs. 2014)	0.47 (0.29, 0.64)			
	Pre vs. post-harvest	-0.55 (-0.71, -0.39)	45.5	1 / 292	< 0.001
	Transect (SD, rand. effect)	0.23 (0.00, 0.41)			
Grasshopper Sparrow / Density in reference	Intercept	-0.02 (-0.11, 0.07)			
	Year (2015 vs. 2014)	0.08 (-0.04, 0.19)	7.1	2 / 292	0.001
	Year (2016 vs. 2014)	0.18 (0.09, 0.28)			
	Pre vs. post-harvest	0.13 (0.04, 0.21)	8.5	1 / 292	0.004
	Transect (SD, rand. effect)	0.05 (0.00, 0.10)			

Table 3. (continued)

Species / Dependent Variable	Independent variables	Coefficient (95% C.I.)	F	df	P
Eastern Meadowlark / Δ density (refugia–reference)	Intercept	-0.11 (-0.24, 0.03)			
	Year (2015 vs. 2014)	0.18 (-0.02, 0.36)	2.0	2 / 292	0.14
	Year (2016 vs. 2014)	0.13 (-0.04, 0.28)			
	Pre vs. post-harvest	0.03 (-0.12, 0.17)	0.1	1 / 292	0.71
	Transect (SD, rand. effect)	0.01 (0.00, 0.11)			
Eastern Meadowlark / Density in refugia	Intercept	0.06 (-0.04, 0.16)			
	Year (2015 vs. 2014)	0.13 (-0.02, 0.27)	1.4	2 / 292	0.24
	Year (2016 vs. 2014)	0.05 (-0.06, 0.17)			
	Pre vs. post-harvest	-0.04 (-0.15, 0.07)	0.6	1 / 292	0.46
	Transect (SD, rand. effect)	0.00 (0.00, 0.08)			
Eastern Meadowlark / Density in reference	Intercept	0.17 (-0.19, 0.04)			
	Year (2015 vs. 2014)	0.05 (-0.20, 0.09)	0.8	2 / 292	0.44
	Year (2016 vs. 2014)	-0.08 (-0.19, 0.04)			
	Pre vs. post-harvest	-0.07 (-0.17, 0.04)	1.6	1 / 292	0.21
	Transect (SD, rand. effect)	0.05 (0.00, 0.12)			

Table 4. Mean density (individuals / ha) in three adjacent hayfields in New Jersey (USA) before and after harvest: 'primary' field in which rectangular unharvested refugia were left, and two adjacent fields that lacked refugia ('north' and 'south' fields; see Fig. 2). Density was computed based on surveys at five 200-m transects in the primary field, and two each in north and south fields. Estimates were corrected for species-specific detection probabilities using distance sampling (see Methods).

Species	Year	North Field (no refugia)			South Field (no refugia)			Primary Field (5 refugia: 5% of area)		
		Density Before Harvest (no./ha)	Density After Harvest (no./ha)	% change	Density Before Harvest (no./ha)	Density After Harvest (no./ha)	% change	Density Before Harvest (no./ha)	Density After Harvest (no./ha)	% change
Bobolink	2014	2.18	0	-100%	1.13	0	-100%	2.14	1.13	-47%
	2015	0.82	0	-100%	0.31	0	-100%	1.58	0.63	-60%
	2016	0[†]	NA[†]	NA[†]	0.48	0	-100%	1.72	0.62	-64%
	Mean	1.50	0	-100%	0.64	0	-100%	1.18	0.79	-57%
Grasshopper Sparrow	2014	0.72	0.26	-64%	0.29	0	-100%	0.29	0.41	42%
	2015	0.71	0.04	-94%	0.46	0.06	-86%	0.62	0.86	39%
	2016	0.30[†]	NA[†]	NA[†]	0.60	0.17	-72%	0.66	0.75	13%
	Mean	0.72	0.15	-79%	0.45	0.08	-86%	0.52	0.67	31%
Eastern Meadowlark	2014	0.05	0	-100%	0.11	0.34	219%	0.17	0.32	95%
	2015	0	0	0	0.08	0.04	-49%	0.15	0.25	73%
	2016	0[†]	NA[†]	NA[†]	0.07	0	-100%	0.10	0.20	97%
	Mean	0.02	0	-50%	0.09	0.13	23%	0.14	0.26	88%

[†] Field planted in row crop (Sorghum Sudangrass) in 2016. Density in this field not included in mean.

Figures

Figure 1. An unharvested patch ('refugium') left for grassland birds in a central New Jersey (USA) hayfield, 3 d after harvest.
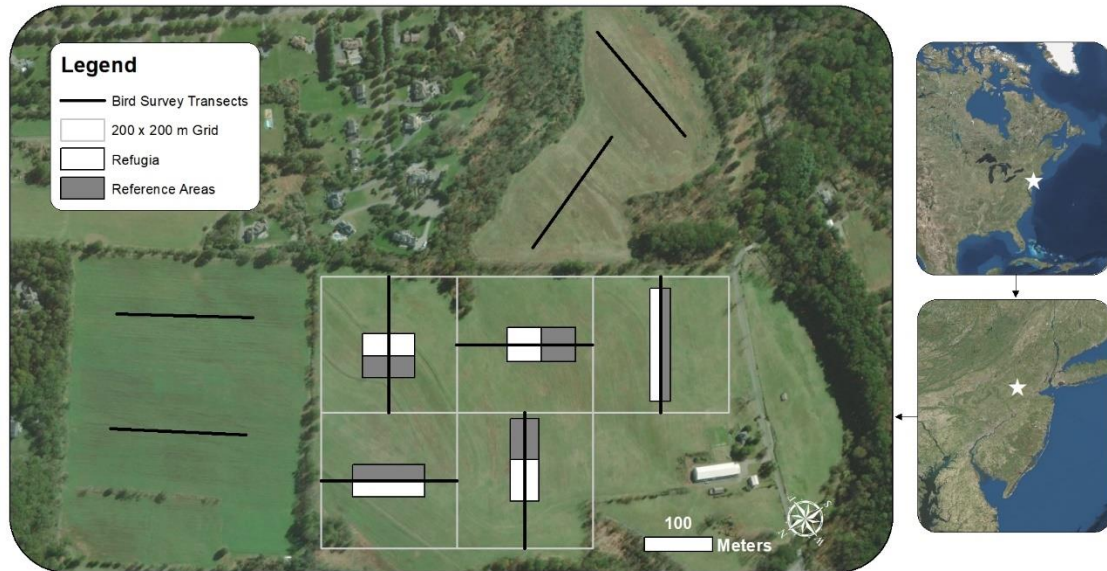
Figure 2. Experimental setup to test the value of uncut patches ('refugia') to grassland birds following harvest in a 23-ha hayfield in central New Jersey, USA, 2014-2016. White rectangles are refugia and gray rectangles are harvested reference areas used to compare relative bird abundance in a before-after-control-impact paired series design. Black lines are 200-m bird survey transects established using the 200 x 200 m grid (light gray boxes). Two additional fields included in the study that lacked refugia ('north' and 'south' fields) are located just beyond the tree lines from the primary field to the left and top of the map, respectively.
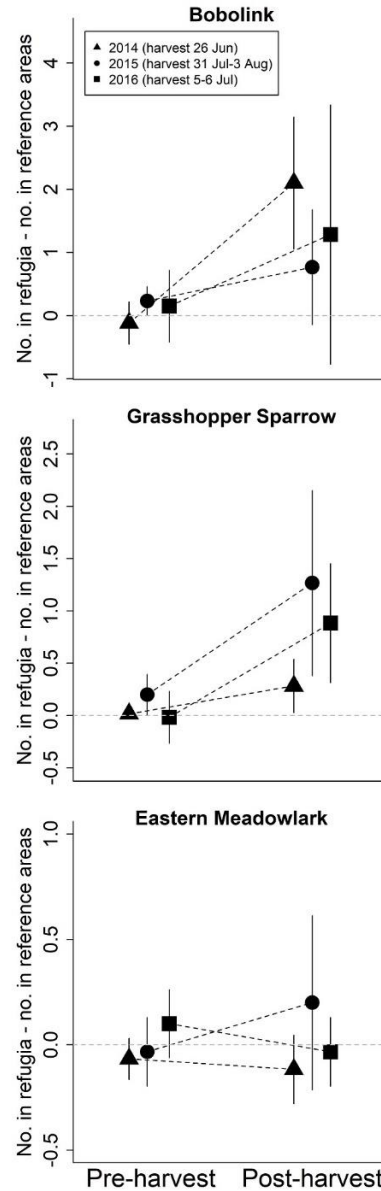
Figure 3. Grassland bird abundance in unharvested refugia and harvested reference areas before and after harvest within a 23-ha hayfield in central New Jersey, USA. Points represent the average difference (± 2 SE) in the number of birds per paired 0.25-ha refugia and reference area, calculated before and after hay harvest (n = 5 for each estimate). The dates of harvest were 26 Jun 2014, 31 Jul–3 Aug 2015, and 5–6 Jul 2016. A before-after-control-impact paired series analysis revealed increased relative usage of refugia by Bobolink (*Dolichonyx oryzivorous*) and Grasshopper Sparrow (*Ammodramus savannarum*), but not Eastern Meadowlark (*Sturnella magna*).

Climate-driven variation in farm management explains population fluctuations in a

grassland songbird: an integrated social-ecological model

ABSTRACT

Efforts to improve conservation outcomes in agricultural landscapes can benefit from a social-ecological systems approach. We used structural equation modelling and public time series data (1994-2015) from the eastern United States to relate the interconnected drivers of farm management decisions and resulting effects on population fluctuations in a declining grassland bird. We found hayfield management – yield and timing – to be important drivers of annual Grasshopper Sparrow (*Ammodramus savannarum*) population growth rate (R^2 = 20%), Yield and harvest timing, in turn, were influenced by rainfall and spring temperatures (R^2 = 51% and 23%, respectively). We found little to no effect of conservation incentive spending on populations, likely due to an inadequate scale of implementation. Large sums are spent annually in many countries to sustain wildlife in agricultural landscapes, while many populations continue to decline. Models such as the one described answer increasing calls for accountability and outcome monitoring of incentive spending, as well as identifying regional conservation policy levers in a systems context.

INTRODUCTION

When conservation programs are viewed as inefficient or unsuccessful they can lose public support and risk being scaled back or abandoned. It is therefore critical to demonstrate and improve the effectiveness of such programs in an adaptive fashion. Such efforts can benefit from a combination of 1) systematic outcome monitoring (Ferraro & Pattanayak, 2006; Purvis et al., 2009) and 2) a social-ecological systems approach (Haberl et al., 2009; Collins et al., 2011). The former allows effect sizes to be estimated for conservation investments, while the latter recognizes that such investments operate within a broader network of social, economic, and ecological drivers. Recent decades have seen progress towards understanding the role of conservation actions within diverse social-ecological systems (e.g., Hughes et al., 2017, Rissman & Gillon, 2017). However, empirical data and models evaluating regional effect sizes of conservation interventions at regional scales within this context remain rare (Ferraro & Pattanayak, 2006, Purvis et al., 2009). Here we present an empirical social-ecological systems analysis using latent-variable structural equation modelling (SEM; Shah, 2008) to measure conservation outcomes and population drivers of a ground-nesting songbird (Grasshopper Sparrow, *Ammodramus savannarum*) in the social-ecological context of agricultural grasslands of the eastern United States.

The conservation of biodiversity on 'working' agricultural landscapes is an area of active social-ecological systems research (Kramer et al., 2017), and one with clear policy implications. Agriculture currently occupies ~40% of terrestrial Earth and continues to expand (Foley et al., 2011). Meanwhile, agricultural intensification to feed a growing population frequently involves management practices that conflict with threatened species inhabiting or adjacent to the agricultural matrix (Donald et al., 2001; Tscharntke et al., 2005; Attwood et al., 2009). These and other environmental impacts of

farming have led to the creation of large federal programs in Europe and North America in recent decades (some exceeding \$5B yr^{-1}) that compensate farmers for altering their management practices to promote biodiversity including birds and other wildlife, as well as to improve other environmental attributes such as water and soil quality (Van Buskirk & Willi, 2004, Batáry et al., 2015). As these programs grow in number and importance worldwide (Kinzig et al., 2011), and as species targeted for conservation have in many cases have continued to decline (Kleijn et al., 2001; Peterjohn, 2003; Attwood et al., 2009; Pe'er et al., 2014), calls to monitor outcomes and improve effectiveness of these programs have amplified (Ferraro & Pattanayak, 2006; Purvis et al., 2009; Kleijn et al., 2011; Briske et al., 2017).

The need for outcome monitoring of agri-environment conservation programs in a social-ecological context is well illustrated by the two largest such efforts, those of the U.S. 'Farm Bill' (\$5.9 billion/yr for 2014-2018) and the European Union's (EU) Common Agricultural Policy (CAP; \$5.7 billion/yr for 2007-2013; Kleijn et al., 2011; USDA ERS, 2018). These programs began in the 1980s and 1990s and consist of monetary incentives for a suite of practices designed to provide ecosystem services including water quality, soil health, and wildlife conservation (Kleijn et al., 2011; Batáry et al., 2015). Land retirement (aka 'set-aside') practices involve taking land out of production for a set number of years (Van Buskirk & Willi, 2004), while working lands (aka 'agri-environmental') practices may include altering harvest timing, planting desirable species, or other 'in-field' measures for lands in active production (e.g., Nocera et al., 2005; Schulte et al., 2017). These programs are designed in part to benefit grassland and other farmland bird populations that depend on agricultural lands to varying extents in many areas. Grassland birds have experienced population declines of >40-60% in the last half century in these regions due in large part to management impacts associated

with agricultural intensification (Donald et al., 2001; Askins et al., 2007; Gregory & Burfield, 2018). For example, the degree of temporal overlap between hay harvests and nesting (Figure 1) may have increased in recent decades as harvests have become earlier and more frequent, leading to greater mortality of eggs and young (Askins et al., 2007; Bock et al., 2013).

Early efforts to evaluate the success of agricultural private-lands programs were based on simple metrics of acreage enrolled (Purvis et al., 2009). Later, comparative studies of populations or communities in enrolled vs. unenrolled land generally found the programs effective at conserving bird populations at local scales (Johnson & Igl, 1995; Van Buskirk & Willi, 2004). However, at the landscape scale, farmland bird populations and other key environmental indicators (e.g., soil and water quality) have continued to decline, leading to increasing calls for evaluation schemes that estimate regional-scale effect sizes of these programs (Askins et al., 2007; Purvis et al., 2009; Kleijn et al., 2011; Pe'er et al., 2014; Briske et al., 2017). If programs are shown to benefit organisms on local but not regional scales, this implies a need for an increase in the area affected and/or a change in how programs are implemented.

In addition to measuring regional effectiveness of conservation programs, it is vital to understand how these conservation interventions operate in the context of the myriad other direct and indirect influences on populations, from climate to social and ecological factors. Integrated social-ecological systems frameworks incorporate drivers of interlinked human and natural systems into the same model (statistical, conceptual, or otherwise). This can be especially useful for suggesting additional conservation actions 'upstream' (distal) of the more obvious proximal factors driving declines (Malawska et al., 2014; Hughes et al., 2017). To date, a relatively small fraction of social-ecological systems analyses has focused on biodiversity conservation (Rissman & Gillon, 2017).

Most approaches to social-ecological systems research in agricultural settings have been non-integrated (i.e., analytically compartmentalized, modelling either the drivers of farmer behavior [Willock et al., 1999; Berger, 2001] or the effects of farming [Perlut et al., 2008; Butler et al., 2010]), and most integrated approaches have been simulation-based rather than empirical (e.g., Mouysset et al., 2011; Malawska et al., 2014). In general, empirical (statistical) and simulation-based modelling are complementary approaches and yield deeper insights when used synergistically (Bruch & Atwell 2015).

Structural equation modelling is an approach with roots in the social sciences that shows promise for empirically analyzing integrated social-ecological system dynamics (Asah, 2008, Grace et al., 2012). For example, it allows the calculation of effect sizes (and associated uncertainty) among a causal network of 'upstream' (distal or exogenous) drivers of conservation-relevant human behaviors, and 'downstream' (proximal or endogenous) effects of those behaviors on conservation outcomes (Asah, 2008; Grace et al., 2012). Non-integrated SEM-based social-ecological approaches have proven effective at analyzing how the various components of agricultural social-ecological systems interact tracing back to the agricultural origins of SEM (Wright, 1925; Willock et al., 1999; Menozzi et al., 2015; Fernández-Giménez et al., 2018). To our knowledge, integrated social-ecological system SEMs applied to agricultural policy evaluation are rare (Chen et al., 2015; Neumann et al., 2017), and such efforts have typically focused on ecosystem- rather than population-level responses (but see Nocera & Koslowsky 2011).

Still fewer studies (SEM-based or otherwise) use a temporally explicit approach, which is essential for long-term systems-level monitoring (Haberl et al., 2009; Collins et al., 2011).

Here we illustrate the use of structural equation modelling to formulate and test explicit hypotheses within a socio-environmental systems context regarding the effects of agricultural policy on animal populations. This is accomplished using public time series data on conservation spending, agricultural practices, land use, climate, and population levels of a grassland bird (Grasshopper Sparrow) in eastern North America.

METHODS

Our process involved gathering state-level public time series data on Grasshopper Sparrow populations, conservation spending, agricultural management, commodity prices, and climate, and relating these in a structural equation modelling framework. The result is an integrated, and temporally explicit, predictive model of 1) farmer management behaviors, and 2) grassland bird populations.

Data sources and processing

Time series data spanning 20 years between 1994 – 2015 (exact range of years depending on time-lags used) were obtained for six states: Pennsylvania, New Jersey, Delaware, Maryland, West Virginia, and North Carolina (see Table 1). These were the only years and states in the Mid-Atlantic region for which we were able to obtain a nearly-complete dataset. The dependent variable in our analysis was the annual population growth rate of Grasshopper Sparrow in each state as estimated by the annual percent change in the state-level North American Breeding Bird Survey population index (Sauer et al., 2017). For other system variables, we sought out all available annual time series data that 1) related to area or management of agricultural grasslands (hay, pasture, idle fields), the primary habitat for Grasshopper Sparrows in the region; or 2) are a potential climatic or economic driver of these dynamics (full variable list in Table 1).

Variable selection was informed by both the agricultural and grassland bird literatures (e.g., Bollinger et al., 1990; Turvey, 2001; Perlut et al., 2008, Nocera & Koslowsky, 2011), as well as by our knowledge of the system. All data were downloaded directly from federal or non-governmental organization websites (Table 1), but some required additional processing and estimation.

We accessed spending data on six Farm Bill-funded conservation practices through an online database made available by Environmental Working Group (https://conservation.ewg.org/): four administered by the United States Department of Agriculture [USDA] Farm Service Agency's [FSA] Conservation Reserve Program [CRP] and two within the USDA's Natural Resources Conservation Service's [NRCS] Environmental Quality Incentive Program [EQIP] and Wildlife Habitat Incentive Program [WHIP]. Based on conversations with regional FSA and NRCS employees and a review of government factsheets, these six practices were judged to be the main agents in the region for idling cropland and implementing wildlife-friendly management in working grasslands (e.g., establishing native grasses or delaying harvests until after the breeding season). Additional details can be found in Supplemental Information. All dollar amounts were adjusted to 2016 dollars using the U.S. Bureau of Labor Statistics Consumer Price Index (USDL BLS, 2018).

Annual estimates of cattle population were available by state, but pasture area was only available at 5-year intervals. To estimate cattle stocking density, we divided annual population counts (measured January 1st) by an estimate of annual pasture area calculated using linear interpolation of the 5-year estimates. These annual estimates of pasture area are believed to improve estimates of stocking density (i.e., by relativizing by approximate area), but were not considered sufficiently fine-grained to act as a proxy measurement for fluctuations in pasture area as a stand-alone variable in the model.

From the 5-yr estimates, pasture area showed a clear increasing trend in all six states, while cattle stocking densities showed a decreasing trend in all states.

Median dates for the first and second hay harvests per year were estimated from weekly National Agricultural Statistics Service (NASS) Crop Progress Report data. These data are in the form of weekly state-level estimates of the cumulative percent of the hay crop harvested as reported to NASS by a network of field observers (often agricultural extension agents). While these data are widely available in the Northeast since 2014, data extending back to the 1990s was only available for the six states included in this analysis and were the limiting factor in this study, geographically. To estimate the ordinal date at which 50 percent of the harvest had been completed, we used linear interpolation of the dates immediately above and below the 50 percent mark (e.g., if 40% of the hay crop was estimated to have been harvested by date X and 60% by date Y, then the estimated median [50%] harvest date would be the mid-point between X and Y). States in which alfalfa (*Medicago sativa*) makes up a significant percentage of the hay crop provided separate progress estimates for alfalfa and grass-dominated hay (and no combined estimate). In these cases, we calculated a weighted average (by area; NASS Crops/Stocks Survey) of the median dates for the two hay types in each year. Both types of hay are used as nesting habitat by grassland birds (Bollinger et al., 1990).

We treated variables related to land use (e.g., area of hay or idle land) differently than variables describing management practices (e.g., stocking rates, harvest timing). We hypothesized that bird population growth rate would be more likely to directly relate to relative changes in area of agricultural grasslands (i.e., annual percent change) than the absolute area. For example, if hayfields are a primary habitat for Grasshopper Sparrow in the region and they double in area from year X_t to X_{t+1}, then we would expect

an increase in population (i.e., positive population growth rate) from year X_{t+1} to X_{t+2} due to more opportunities for reproduction in year X_{t+1}. For agricultural management variables, we hypothesized that the level (i.e., 'better' or 'worse' conditions each year) would affect growth rate into the next year. For example, hay harvesting and trampling by cattle are known to negatively affect nesting success and/or adult survival (Perlut et al. 2008). We therefore expected years with more-frequent harvesting or higher cattle stocking densities would be followed by years of lower population growth.

Three variables had missing data: 2 values each in the median first (HARV1) and second (HARV2) hay harvest dates, and 6 values in conservation spending (SPEND, ΔSPEND; Table 1). We imputed missing values using the R package 'Amelia' which accommodates hierarchical time series data, creating five complete imputed datasets to evaluate potential effects on our final conclusions (Honaker et al., 2011).

Time series data processing

Time series data should be stationary (i.e., stable mean and variance over time) to evaluate covariance relationships in a linear modeling framework; therefore, we began by examining all series visually for trends. The series were believed to include both trend- and difference-stationary processes, so we chose the approach of taking the first difference of all series (i.e., $X_t - X_{t-1}$). This transformation can effectively remove trends and serial autocorrelation in series generated by both trend- and difference-stationary processes, allowing them to be related in a single analysis (Hyndman & Athanasopoulos, 2018). Following Haest et al. (2017), we used Augmented Dickey-Fuller [ADF] tests (up to lag 1) to test for stationarity (i.e., a unit root) in the resulting differenced series, and the Durbin-Watson test (up to lag 2) to test for serial autocorrelation of residuals from the four main SEM sub-models (i.e., those with the dependent variables describing hay yield, harvest timing, change in hayfield area, and

population growth rate) using manifest variables only. We further evaluated series with p-values > 0.05 for ADF tests (n = 19 of 78 series) for stationarity using Kwiatkowski–Phillips–Schmidt–Shin (KPSS) tests – designed as a compliment to ADF tests (Kwiatkowski et al., 1992) – and visually examined all series, as well as histograms and autocorrelation function plots of sub-model residuals. These tests, performed state-by-state, indicated stationarity in all but two series within one variable (the Maryland and Pennsylvania cattle stocking rate [CATTLE] series) and no autocorrelation in residuals in all 24 sub-models evaluated. The differenced cattle stocking rate data for Maryland and Pennsylvania showed an increasing trend that could likely be eliminated by second order differencing; however, this would require mixing differencing orders in the model which can make interpretation difficult (Hyndman & Athanasopoulos, 2018). Furthermore, cross-correlation of two time series (in this case cattle stocking rate and population growth rate) is not problematic if one of the two is stationary and free of autocorrelation (Shumway & Stoffer, 2017, p. 31). We therefore chose to leave this variable in the final model without further transformation.

Structural Equation Modelling

A structural equation model was constructed based on the logical framework ('meta-model') in Figure 2, and following procedural guidance in Grace (2006, Appendix A) and Grace et al. (2010, 2012). Grasshopper Sparrow populations were hypothesized to be affected by five agricultural variables with available data, which in turn were affected by four climate and two economic factors (see Table 1). We examined bivariate relationships before constructing the full structural equation model to look for evidence of non-linearities, non-normality, and outliers, and adjusted model structure prior to the final iteration on theoretical grounds and without examining SEM modification indices (Grace, 2006).

Grasshopper Sparrows nest in their first year after hatching and can experience high rates of nest loss due to agricultural management activities (Vickery, 1996). Thus, we based the time lag structure of our model on the prediction that agricultural conditions during a given year would be most likely to have same-year effects on Grasshopper Sparrow reproduction and survival, which would be evidenced by lower population growth rate the following year, i.e., agricultural conditions in year X_t affect population change from year X_t into X_{t+1} (Figure 2). This lag structure matches that used by Nocera and Koslowsky (2011) to document the effects of hay harvesting on grassland bird populations at a continental scale. Climate and conservation spending were hypothesized to have same-year effects on agricultural management, so these were also lagged one year, while one economic variable (the relative profitability of hay [PROFIT]; Table 1) was lagged an additional year as farmers' decisions on what to plant were assumed to stem from information on potential profits from the previous year. Exploratory analysis suggested no improvement from including lags beyond one year or of a moving 2- or 3-year average of relative profitability.

We used a latent variable approach to better reflect the hypothesized causal structure of the data, rather than a manifest-variable-only (i.e., path analysis) approach (Grace 2006). For example, the average yield of hay ($Mg \cdot ha^{-1}$) is not thought to directly affect bird reproduction, but rather is likely an indicator of an unmeasured (i.e., latent) variable describing the average number of harvests per season per hectare. Similarly, we specified the median dates of the first and second hay harvests as two correlated measurements of a latent variable, 'hay phenology', the relative timing of harvest activities in each year. Measurements of 'idle' land – a category which includes lands 'retired' via government programs – were only available at a 5-year frequency (USDA NASS, 2012). We therefore specified annual change in conservation spending as a

'second order' indicator (Grace et al., 2010) of a latent variable for the change in idle land area. This was based on exploratory analyses of the 5-year data revealing that conservation spending per ha of cropland is significantly related to the area of idle land and land enrolled in federal programs (Generalized Linear Mixed Model with year as a random variable: $P < 0.003$, GLMM-R^2 = 59% and 41%, respectively).

Besides making causal assumptions explicit, another benefit of using a latent variable approach is the ability to assess the effects of measurement error in predictors. While standard structural equation models assume perfect (1:1) measurement of all single-indicator latent variables – including all latent variables in our primary analysis except 'Hay Phenology', which has two indicators – it is also possible to add assumptions regarding varying levels of measurement error (Grace, 2006). We assess the effects of adding an assumption of 20% measurement error (i.e., a Pearson correlation with the unknown 'true' variable of 0.89) into key variables that we believe most likely to represent imperfect measurements: yield, spending, and population growth rate.

Structural equation modelling was carried out using the 'lavaan' and 'lavaan.survey' packages in R to specify the model and adjust for nested data structure (i.e., years within states), respectively (Rosseel, 2012, Oberski, 2014). Before running the analysis, we scaled all differenced variables as needed by dividing them by a constant, so that their standard deviations fell between 0.1 and 10 to avoid fitting problems (Grace, 2006). We estimated model fit (chi-square statistic) and parameter standard errors using the robust maximum likelihood estimator in lavaan.survey, which relaxes strict assumptions of normality (Oberski, 2014). We present both standardized and unstandardized path coefficients and accept significance at $P = 0.05$. All analyses were performed using R v. 3.5.1 (R Core Team, 2018).

RESULTS

From 1996-2015, Grasshopper Sparrow populations declined at an average rate of -3.5% · yr^{-1} in the six-state study area, with a range of means of -8.5% · yr^{-1} in West Virginia to 2.1% · yr^{-1} in Delaware, the only state to experience positive population growth (Table 2). Variability (SD) in annual growth rate ranged from 3.1 in North Carolina to 9.1 in West Virginia. Spending by state averaged $2.77 · ha of cropland^{-1} · yr^{-1} (range $0.31 – 8.97 · ha^{-1} · yr^{-1}) and averaged $18.9 M · yr^{-1} for the 6-state region (range: $8.4 – 26.5 M · yr^{-1} from 1995-2014). States also exhibited variation in agricultural land use and management means and trends over the 20-year study period (Table 2).

The primary structural equation model (Figure 3) had adequate fit with X^2 = 39.6 – 44.8 (df = 37, P > 0.17) among all five imputed versions of the dataset. Results are presented from a single imputed version (the last run) unless otherwise noted. Annual Grasshopper Sparrow population growth rate was negatively related to the latent variable '# Hay Harvests' (indicated by the manifest variable hay yield [YIELD]) as well as the timing of hay harvests in the previous year (as indicated by the median first [HARV1] and second [HARV2] hay harvest dates; R^2 = 20%). Standardized path coefficients for these variables (with unstandardized coefficients in original units ± SE in brackets) were -0.32 [-3.92 ± 1.90] and -0.20 [-0.20 ± 0.05], respectively. This equates to an approximately one percentage point reduction in average population growth rate predicted for every ~250 kg increase in yield or 5-d delay in harvest. Yield, in turn, was predicted by spring and summer rainfall (R^2 = 51%), and hay harvest phenology by spring temperatures (R^2 = 23%). More rain was associated with greater yields, with coefficients of 0.30 [0.08 ± 0.03] and 0.62 [0.14 ± 0.03] for spring and summer rainfall, respectively. Later harvests were associated with cooler springs, with the coefficient (-0.38 [-0.023 ± 0.048]) predicting a two-day earlier harvest for every 100 degree-day

increase through 31 May. The only relationship to differ based on which version of the imputed dataset version was used was a negative relationship between conservation spending and hayfield area ($R^2 = 7\%$). The p-value for this result was < 0.05 in four out of the five imputed datasets (-0.20 to -0.08, [-0.057 to -0.023], $P < 0.001 – 0.043$), and > 0.05 in one (-0.14, [-0.040]; $P = 0.11$). Conservation spending was not directly or indirectly (i.e., via hayfield area or hay harvest phenology) associated with Grasshopper Sparrow population growth rate ($P > 0.31$). No other path coefficient in the model was significant (full model results are summarized in Figure 3 and Table 3).

Introducing an assumption of 20% measurement error into measurements of hay yield, conservation spending, and population growth rate resulted in moderate improvements in model R^2 values. The latent variable 'Δ Population' increased from 20 to 24% and '# Hay Harvests' from 51 to 65% compared with the model without measurement error in Figure 3. The R^2 values for the latent variables 'Hay Phenology' and 'Δ Hayfield Area' remained unchanged.

DISCUSSION

Our analysis revealed new insights into connections between climate, farm management decisions, and population fluctuations in a declining grassland bird. More broadly, we demonstrate a viable approach to empirical social-ecological systems monitoring of regional conservation outcomes. Our failure to detect a direct or indirect effect of conservation spending could highlight the need for programmatic changes to reverse declines, or alternatively a need for more accurate spending data, both of which could improve conservation efforts. The use of latent variables was effective at highlighting data gaps and allowing exploration of the role of imperfect measurement. In the long term, gathering complete and accurate data for landscape-scale systems-based

monitoring programs is a considerable challenge requiring coordinated efforts among diverse agencies and groups. But where data are already available (or the resources required to collect it), the general approach is readily portable to other regions, species, and systems.

Farming effects on bird populations

It has been widely demonstrated that intensification of agricultural production following World War II has contributed to grassland bird population declines in Europe and North America (Chamberlain et al., 2000; Donald et al., 2001; Murphy, 2003). However, this effect has typically been viewed as a relatively static phenomenon exhibiting mainly spatial variation, rather than as a dynamic system in which populations respond to an annually fluctuating farming environment. For example, in hayfield systems (for which we found greatest effect sizes in our model), the effect of hay harvest timing on grassland bird populations at a regional level in a given year ultimately depends on the full temporal overlap of harvesting activities with nesting phenology (Figure 1). Variation in the timing and frequency of hay harvesting has been widely demonstrated to affect grassland bird nest survival on a field-by-field basis (e.g., Nocera et al., 2005; Perlut et al., 2008; Grüebler et al., 2012), and at a continental scale (Nocera & Koslowsky, 2011), but no other study to our knowledge has quantified these effects on an inter-annual basis at regional scales where they may be most useful from a conservation standpoint. This is the scale, for example, on which responsibility is delegated in relevant government agencies such as the U.S. Fish and Wildlife Service and USDA.

Moving the needle to stop the Grasshopper Sparrow populations decline in our study region (-3.5% yr^{-1}) and prevent local extinction may require a significant increase in conservation spending or a different allocation of current spending levels. Our finding

that populations in the Mid-Atlantic U.S. showed biologically meaningful reductions in

population growth rate following years of higher hay yields (~ 4 percentage points lower

per metric ton increase) and later harvests (~ 2 percentage points lower per 10-day

delay in harvest) is significant in that it provides landscape-scale targets to increase

population growth. Consider, for example, this simplified scenario: imagine that we can

compensate farmers to reduce hay yields in the region in a way that affects population

growth as in our model (e.g., by taking fewer harvests during the breeding season). If

this was the case, then forgoing 0.9 Mg · ha^{-1} · yr^{-1} of hay harvest would be required to

bring the regional growth rate up to zero from -3.5% (i.e., given a slope of 3.9

percentage points · Mg^{-1}). Such an effort – ignoring unforeseen thresholds, feedbacks,

or non-linearities (Liu et al., 2007) – would cost ~\$176 million · yr^{-1} when applied to the

1.2 million ha of hayfields in the region (USDA NASS, 2012), over 6 times higher than

the maximum annual expenditure observed during our study period (\$27 million · yr^{-1}).

However, such a drastic reduction in yield (~1-2 SD depending on the state; Table 2)

may not be necessary due to 'working lands' approaches that compensate farmers for

altering harvest timing (e.g., harvesting outside of the breeding season) not necessarily

the total amount harvested (Nocera et al., 2005).

Uncertainties in our model likely come from two sources. While farm

management variables explained about 20% of variation in population growth rates

(Figure 3), unexplained variation may have come from both measurement error and from

important variables left out of the model (e.g., climate conditions on the wintering

grounds; Woodworth et al., 2017). Data limitations highlighted by our model include the

lack of annual estimates of the average hay harvest frequency per field, and the area of

idle fields and pastures. These required the use of proxy variables that likely added

uncertainty. For example, hay yield was used as a 1:1 indicator for a latent variable

describing the average hay harvest frequency, though in reality yield contains information about both the number of harvests and the average biomass per harvest (Turvey, 2001). Similarly, even though our measure of conservation spending on the six grassland programs was correlated with idle land area, it is an imperfect indicator as it also contained an unknown proportion of spending for what are better classified as 'working-lands' practices (e.g., plantings, invasive species removal).

Other sources of uncertainty come from the nature of working with time series data and dynamic systems. For example, it is important to be aware that the effect sizes observed in our model represent correlations between detrended fluctuations in agricultural variables and population growth rates. Therefore, the level of a dependent variable (i.e., the average value around which it fluctuates) could change over time such that the variable becomes more or less influential (i.e., changes effect size), something best handled analytically using dynamic linear models (Shumway & Stoffer, 2017). Non-linearities and thresholds are also possibilities to be mindful of when extrapolating beyond observed data (Liu et al., 2007; Collins et al., 2011). Even so, our approach of documenting a 'snapshot' of regional effect sizes linking system variables, some of which could be influenced by policy and management actions, is a useful start.

The role of conservation spending

The lack of effect observed between conservation spending and hayfield management variables was surprising, and but may signify an inadequate scale of implementation rather than a lack of effectiveness of individual practices. At field-scales, employment of these practices is known to positively affect bird populations by altering harvest timing, improving habitat structure, or other means (e.g., Johnson & Igl, 1995; Van Buskirk & Willi, 2004; Nocera et al., 2005; Perlut et al. 2008). Further, Farm Bill spending is low in the eastern U.S. relative to other regions. Estimates of spending on

the six Farm Bill practices included in our study averaged $2.8 \cdot ha^{-1}$ of cropland by state (range: $0.3 – $9.0; Table 2), with a ratio of land enrolled in government conservation programs to total cropland area of 2.9% (range: 1.1 – 5.3%; USDA NASS, 2012). In contrast, a mid-western state such as Iowa spends $13.6 \cdot ha^{-1}$ on the same practices, with an enrolled land to cropland ratio of 6.9%.

It is also possible that the lack of detectable effects from conservation spending could relate to measurement error. We were not able to include state-level spending on Farm Bill-like programs due to data limitations, and this spending may have been substantial in some states and years. For example, in at least some states, an unknown portion of the federally-funded but state-administered Landowner Incentive Program (2003-2007) was used for such programs (e.g., NJDEP, 2014). The federal spending data we used also contained some uncertainty, including the fact that WHIP/EQIP spending can be used to fund for a variety of grassland management activities besides harvest restrictions (e.g., invasive species and shrub control, native plantings), as well as some non-grassland activities (e.g., shrubland management). These activities formed an unknown portion of the WHIP/EQIP funding in our study. Because of these uncertainties, our current spending measure is best viewed as an index. Together, these shortcomings and the previously discussed data gaps and limitations highlight the need for better and more coordinated data tracking and availability, something also noted in European farmland conservation efforts (Chamberlain et al., 2000).

The role of climate

Climatic drivers of annual farm management decisions appear to be well-known and appreciated in the agricultural and popular literature (e.g., Klinkenborg, 1986; Turvey, 2001), but lacking from the grassland bird conservation literature (Pearce-Higgins & Gill, 2010). We found hay yields were higher in years with more spring and

summer rainfall, presumably due in part to better growing conditions allowing farmers a greater number of harvests in a season (Turvey, 2001). Years of high yield were in turn followed by poor population growth in our model, presumably due to a greater harvest frequency leading to increased egg and young mortality and/or poor adult survival (e.g., Perlut et al., 2008). Our model also predicted earlier hay harvests in warmer springs (March-May), with resulting positive effects on bird populations (Figure 3). It is possible that during these 'early years' the date of first harvest shifts enough to precede the start of the Grasshopper Sparrow nesting season (Figure 1) or at least early enough into the season that re-nesting becomes more likely (Vickery, 1996). Other species with different nesting phenology may fare differently.

Knowing in advance which years are likely to be 'good' and 'bad' for grassland bird population growth also raises intriguing possibilities. For example, it may be possible to dampen population variability, a known risk-factor for extinctions, via dynamic conservation spending. As data on two exogenous factors controlling the hay harvest in this system (spring temperatures and precipitation) are known by 31 May each year, a nimbler version of current conservation incentive programs could in theory respond by adjusting spending based on these parameters (e.g., spending more in 'worse' years).

Importantly, climate fluctuations and future climate change are likely to affect not only crop growth and associated farming activities, but also to cause phenological shifts in bird nesting. How the magnitude of these shifts varies among species and how they will interact with shifts in agricultural phenology in a changing climate are still poorly understood (Pearce-Higgins & Gill, 2010). These are important areas for future research.

Social-ecological system monitoring for conservation

In both the US and EU, calls for improvements to evaluating biodiversity impacts of Farm Bill and CAP programs have stressed a need for going beyond simple metrics of local-scale effectiveness and participation rates towards outcome monitoring at broader spatial and temporal scales (Purvis et al., 2009; Briske et al., 2017). Within USDA, the Natural Resources Analysis Group and the Conservation Effects Assessment Project (CEAP) are actively sponsoring and compiling research on the effectiveness of Farm Bill conservation spending (Briske et al., 2017). Our analysis adds to this growing effort to improve accountability in private landowner conservation initiatives by providing a systems framework in which to evaluate outcomes at the landscape scale.

Building effective social-ecological system-based monitoring programs at landscape scales will take careful consideration of variables and system dynamics (Liu et al., 2007; Collins et al., 2011). Latent-variable SEM approaches can be valuable empirical supplements to the currently-popular simulation-based approaches (reviewed in Malawska et al., 2014). Gathering the required data and assembling theoretical frameworks for such large-scale systems-based monitoring efforts may not be easy, requiring a new scale of cooperation among partners in academia, government agencies, and other stakeholder groups to succeed. But such challenges will be needed to confront the myriad social-ecological challenges we face – from biodiversity loss to climate change – in an increasingly human-influenced world.

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Tables

Table 1. Description of time series variables used as 'manifest' variables in a structural equation model describing Grasshopper Sparrow (*Ammodramus savannarum*) population growth rate in the Mid-Atlantic U.S. All data are at the state-level spatial scale, the finest spatial extent available annually for all variables. Abbreviations used are as follows: BLS = Bureau of Labor Statistics, FSA = Farm Service Agency, NASS = National Agricultural Statistics Service, NOAA = National Oceanic and Atmospheric Administration, USDA = United States Department of Agriculture, USGS = United States Geological Survey.

Variable	Description	Units	Processing	Lag	Source & Years
ΔBBS	Annual change (growth rate) in Grasshopper Sparrow Breeding Bird Survey population index.	Percent	Expressed as growth rate (year-over-year percent change).	0	USGS North American Breeding Bird Survey (Sauer et al. 2017), 1996-2015
ΔHAY	Annual change in area of hayfields	Percent	Expressed as growth rate (year-over-year percent change).	1	USDA NASS Crops/Stocks Survey, 1995-2014
ΔSPEND	Annual change in spending on 6 federal programs used to fallow land and delay hay harvests. (Correlated with 5-year estimates of % idle land and land enrolled in government programs, see Methods.)	Percent	Expressed as percent change from previous year: $[100*(X_{t+1} - X_t) / X_t]$, where X = 2016 USD.	1	Environmental Working Group Conservation Database; USDA FSA table of average rent per acre by year; U.S. BLS Consumer Price Index, 1995-2014

Table 1. (continued)

Variable	Description	Units	Processing	Lag	Source & Years
SPEND	Spending per hectare of cropland on 6 federal programs used to fallow land and delay hay harvests.	US dollars (2016) per ha of cropland	Divided spending (in 2016 USD) by annual estimate of cropland area (ha) in the state.	1	Environmental Working Group Conservation Database; USDA FSA table of average rent per acre by year; US BLS Consumer Price Index; USDA NASS Crops/Stocks Survey, 1995-2014
HARV1	Date at which 50% of the first-cutting hay harvest was completed in the state.	Ordinal date	Interpolated from weekly '% harvested' estimates.	1	USDA NASS Crop Progress/Conditions Reports, 1995-2014
HARV2	Date at which 50% of the second-cutting hay harvest was completed in the state.	Ordinal date	Interpolated from weekly '% harvested' estimates.	1	USDA NASS Crop Progress/Conditions Reports, 1995-2014
YIELD	Yield of hay harvested; a proxy variable for harvesting frequency	Mg / hectare	Converted from tons per acre.	1	USDA NASS Agricultural Yield Survey, 1995-2014
CATTLE	Estimated cattle stocking density.	Head / hectare of pasture	Divided annual cattle population (January 1st) by estimated pasture area (linear interpolation of 5-year estimates)	1	USDA NASS Cattle Inventory, 1995-2014

Table 1. (continued)

Variable	Description	Units	Processing	Lag	Source & Years
PROFIT	Ratio of gross per-ha profitability of hay over that of corn or soy (the larger of the two).	Ratio	Gross per-ha profitability = annual average unit price times yield per ha. All prices in 2016 USD.	2	USDA NASS & Economic Research Service Agricultural Resource Management Survey and Agricultural Yield Survey, 1994-2013
PRECSP	Spring precipitation totals (March-May)	Inches	NA	1	NOAA National Centers for Environmental Information, 1995-2014
PRECSU	Summer precipitation totals (June-July)	Inches	NA	1	NOAA National Centers for Environmental Information, 1995-2014
RAIND	Number of days with >0.1 inches of precipitation between 15 May and 15 June.	Days	NA	1	PRISM Climate Group, Oregon State University (http://prism.oregonstate.edu), 1995-2014
GDD	Growing degree-days above 10 °C (Jan-May)	Degree-days	NA	1	PRISM Climate Group, Oregon State University (http://prism.oregonstate.edu), 1995-2014

Table 2. Mean values and temporal trends (slope) by state for Grasshopper Sparrow (*Ammodramus savannarum*) population growth rate (1996-2015) and select agricultural variables (1995-2014).[a]

State[b]	Grasshopper Sparrow Pop. Growth Rate ($\% \cdot yr^{-1}$) mean (SE)	trend (SE)	Conservation Spending (2016 USD · ha of cropland^{-1}) mean (SE)	trend (SE)	Median 1st Hay Harvest Date mean (SE)	trend (SE)	Hay Yield ($Mg \cdot ha^{-1}$) mean (SE)	trend (SE)	Hayfield Area Growth Rate (%) mean (SE)	trend (SE)	Cattle Density (head · ha of pasture^{-1}) mean (SE)	trend (SE)
DE	2.2 (2.0)	0.07 (0.35)	0.3 (0.0)	-0.01 (0.01)	23 May (3 d)	-0.83 (0.39)	6.6 (0.2)	-0.09 (0.04)	0.4 (3.4)	-0.28 (0.59)	3.5 (0.2)	-0.16 (0.01)
MD	-4.0 (1.5)	0.31 (0.26)	4.4 (0.3)	0.04 (0.06)	29 May (2 d)	-0.63 (0.31)	5.9 (0.1)	-0.04 (0.02)	0.4 (2.4)	-0.09 (0.43)	1.8 (0.1)	-0.10 (0.01)
NC	-0.8 (0.7)	-0.03 (0.12)	0.9 (0.1)	-0.07 (0.01)	20 May (1 d)	0.01 (0.22)	5.0 (0.1)	0.00 (0.02)	2.5 (2.2)	-0.12 (0.39)	1.4 (0.2)	-0.12 (0.01)
NJ	-3.5 (1.5)	0.06 (0.26)	1.4 (0.2)	0.09 (0.03)	13 Jun (3 d)	0.38 (0.57)	4.7 (0.1)	0.01 (0.02)	-0.5 (0.9)	-0.05 (0.16)	1.0 (0.1)	-0.07 (0.00)
PA	-6.3 (0.9)	0.07 (0.16)	9.0 (1.0)	0.64 (0.10)	11 Jun (1 d)	-0.74 (0.18)	5.1 (0.1)	0.02 (0.02)	-1.4 (1.3)	-0.04 (0.24)	2.8 (0.2)	-0.14 (0.01)
WV	-8.5 (2.0)	0.08 (0.36)	0.6 (0.1)	0.07 (0.02)	17 Jun (2 d)	-0.27 (0.29)	4.1 (0.1)	-0.01 (0.02)	0.6 (0.7)	0.02 (0.13)	0.5 (0.0)	-0.03 (0.00)
Mean	-3.5	0.09	2.8	0.13	3 Jun	-0.35	5.3	-0.02	0.3	-0.10	1.9	-0.10

[a] Sample size is 20 for all estimates except Conservation Spending (all states) and Median 1st Hay Harvest Date (DE and NJ) for which n = 19.

[b] DE = Delaware, MD = Maryland, NC = North Carolina, NJ = New Jersey, PA = Pennsylvania, WV = West Virginia.

Table 3. Results from a structural equation model describing the interrelationships between climate, farming, economics, and Grasshopper Sparrow (*Ammodramus savannarum*) population growth rate in a six-state region of the Mid-Atlantic U.S. (1996-2015). Variable names correspond to the latent variables shown in circles in Figure 3. Descriptions of the manifest variables on which they are based are in Table 1.

Dependent variable	R^2	Independent variable	Coefficient (standardized)	Coefficient ± SE (unstandardized)	z-value	P-value
Δ Pop.	20%	# Hay Harvests	-0.32	-3.92 ± 1.90	-2.1	0.039
		Hay Phenol.	-0.20	-0.20 ± 0.05	-4.1	< 0.001
		Δ Idle Field Area	-0.08	-0.02 ± 0.02	-1.0	0.312
		Δ Hayfield Area	0.01	0.01 ± 0.10	0.1	0.922
		Cattle Density	0.19	13.88 ± 8.56	1.6	0.105
# Hay Harvests	51%	Spring Rainfall Total	0.30	0.07 ± 0.02	3.0	0.002
		Summer Rainfall Total	0.62	0.14 ± 0.03	5.4	< 0.001
Hay Phenol.	23%	Spring Growing Degree Days	-0.38	-0.02 ± 0.00	-4.8	< 0.001
		Rainy Days During 1st Hay Harvest	0.24	0.64 ± 0.40	1.6	0.110
		Conserv. Spend.	-0.13	-2.14 ± 1.60	-1.3	0.181
Δ Hayfield Area	7%	Hay Relative Profit per Acre	-0.18	-8.69 ± 6.63	-1.3	0.190
		Δ Conserv. Spend.	-0.20	-0.06 ± 0.03	-2.0	0.042

Figures
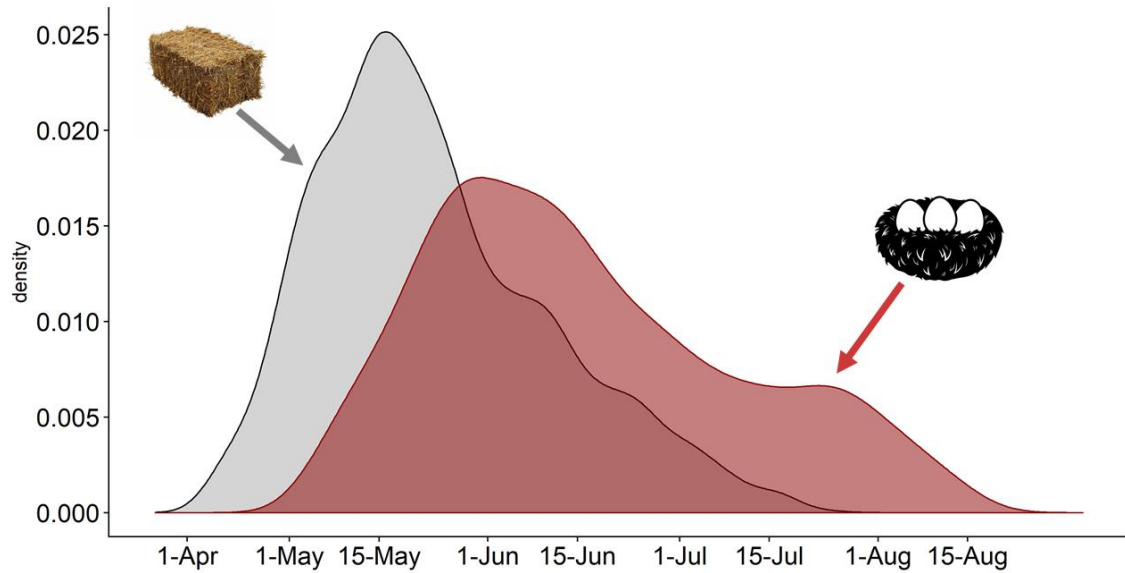
Figure 1. Temporal overlap between phenology of the first hay harvest (gray) and active Grasshopper Sparrow (*Ammodramus savannarum*) nests (red). Y-axis and shaded areas show probability density based on 'first cutting' hay harvests in North Carolina, USA (1991-2016) and estimated number of Grasshopper Sparrow nests active in Oklahoma, USA (1992-1996). These two states are at a comparable latitude (36.6° N vs. 35.6° N). Nest data are from Reinking et al. (2009); see Supplemental Information for processing methods.

Figure 2. Meta-model showing hypothesized relationships between measured and unmeasured components of the grassland bird social-ecological system. Temperature and precipitation can influence farm management practices directly by dictating field conditions for the harvest and indirectly via crop growth. Conservation incentive programs and crop prices can also influence management decisions and choices of which crops to plant. Management activities (e.g., harvest timing and frequency) can affect population growth rate the following year by impacting reproduction or survival. Text below icons represent time lags. Icons: Noun Project contributors (Anton, S. Demushkin, G. Furtado, Hamish, Humantech, P. Rozenberg)

Figure 3. Structural equation model of the relationships between annual climate and economic factors (top row), farm management (middle row), and Grasshopper Sparrow (*Ammodramus savannarum*) population growth rate in the Mid-Atlantic United States, 1996-2015. Circles represent latent variables as indicated by measured ('manifest') variables (Table 1) shown as rectangles. Asterisks indicate temporal lags relative to population growth rate (* = lag 1 year, ** = lag 2 years). Solid and dashed arrows indicate effects below or above the significance threshold of P = 0.05, respectively. Standardized coefficients are shown near significant pathways; all coefficients are presented in Table 3.The hierarchical structure of the model (variables nested within states) is not shown in the diagram for clarity.

SUPPLEMENTAL MATERIAL

Supporting Information S1. Additional methods for conservation spending data

processing

Supporting Information S2. Methods used to create Figure 1 (temporal overlap

between hay harvesting and nesting)

References

SUPPORTING INFORMATION S1: Additional methods for conservation spending data

processing

Methods

Specific CRP practices included: 1) "Establishment of permanent introduced grasses

and legumes" (practice CP-1); 2) "Establishment of permanent native grasses" (practice

CP-2); 3) "Vegetative cover - grass - already established" (practice CP-10); and 4) "State

Acres for Wildlife Enhancement – Grass" (practice CP-38E). Practices within

WHIP/EQIP included: 1) "Upland Wildlife Habitat Management" (practice 645); and 2)

"Early Successional Habitat Development/Management" (practice 647). Spending data

was available for the two WHIP/EQIP practices, while only acreage data was available

for the four CRP practices. To estimate dollar amounts for the CRP practices we

multiplied acres by annual state-level estimates of average CRP rents paid per acre

available from a separate database maintained by FSA (USDA FSA 2018). To make

data comparable across states, we relativized spending by the amount of cropland in the

state (i.e., 2016 USD · ha of cropland-1).

SUPPORTING INFORMATION S2: Methods used to create Figure 1 (temporal overlap between hay harvesting and nesting)

Methods

To visualize the relationship between hay harvest phenology and Grasshopper Sparrow nesting activity we computed probability density functions (Wickham 2016) for a sample of nest initiation dates in Oklahoma (1992-1996), as well as the date of first hay harvest in North Carolina (1991-2016), approximately at the same latitude (36.6° vs. 35.6°). Nesting data was extracted from a frequency distribution of 129 first-egg dates of Grasshopper Sparrow nests in Reinking et al. (2009). From this data, we estimated the number of nests active per day by assuming 1) half the nests in each ~14-d date bin were initiated as two evenly-spaced cohorts within the period, and 2) the number of active nests in each cohort declined each day based on an average nest survival probability value of 0.96, and 3) surviving nests persisted up to a maximum age of 23 d (the full nest cycle; Vickery 1996). This produced an estimated distribution of the number of nests active, and therefore vulnerable to destruction by hay machinery, on a given date, rather than simply a distribution of initiation dates.

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Shifting geographies of spatial synchrony in North American grassland birds: a window into regional population drivers and vulnerabilities

ABSTRACT

Investigations into the geography of population dynamics, besides the usual growth rates and trends, can provide useful tools to inform conservation efforts, revealing hidden regions of common population drivers, metapopulation vulnerability, or other phenomena. Spatial synchrony, defined as the correlated fluctuations of spatially separated populations, can be caused by (among other things) regional fluctuations in natural and anthropogenic environmental population drivers. We examined the geography of spatial synchrony, and decadal changes in these patterns, for North American grassland birds, which are experiencing widespread declines. Our aim was to identify regions that have changed in synchrony, possibly due to intensification of agriculture, climate change, or interactions between the two. We found increasing synchrony in 15 (79%) of 19 species examined, and a significant increase overall across species. Examining the geography of these changes, we identified one major region of increasing and one of decreasing spatial synchrony: the southern Great Plains and the Northeast, respectively. In each region, most change in synchrony was driven by ~6 species (out of 9-12 present), while other species showed no clear trend. Our approach shows promise for highlighting geographical areas of interest for further investigation into mechanisms and population drivers. This work also adds to a growing literature suggesting global change is resulting in increased synchrony in population dynamics, generally, with broad implications for diverse phenomena from extinction risk to pest outbreaks.

INTRODUCTION

Rich spatiotemporal abundance data exist for some declining guilds of species. Yet conservation biologists frequently neglect to go beyond identifying regional population trends to explore the geography of less-appreciated but potentially revealing population dynamics such as spatial synchrony (Walter et al. 2017). Careful study of spatial synchrony – the correlated fluctuations of geographically separate populations – has the potential to reveal regional population drivers (Sheppard et al. 2016) and extinction vulnerability (Schindler et al. 2010), and to aid in conservation planning by putting these regions on a map (Michel et al. 2016). Spatial population synchrony is increasing in diverse taxa and has been associated with climatic change (Koenig and Liebhold 2016; Sheppard et al. 2016), but the geographies of these changes have rarely been examined (Walter et al. 2017). For example, a 50-year increase in spatial synchrony has been documented for winter populations of North American birds (~65% of species studied), yet geographical patterns in these changes have not to our knowledge been previously documented (Koenig and Liebhold 2016). We aim to contribute to this need by examining the geography of decadal changes in population synchrony in a guild of declining species, grassland-obligate birds in North America.

Grassland birds in North America have been in consistent decline since at least the 1960s due to grassland conversion, intensified agricultural management, and potentially climate extremes, all of which have accelerated in recent decades (Askins et al. 2007; Zuckerberg et al. 2018). As these are all regional phenomena, they have the potential to cause 'Moran effects' (Moran 1953), defined as environmentally-driven spatial synchrony in abundance. In grassland birds, regional climate could drive populations by affecting survival and reproduction directly (Gorzo et al. 2016; Woodworth et al. 2017; Zuckerberg et al. 2018) or indirectly by affecting agricultural

management which has the potential to affect habitat quality on large spatial scales (Pearce-Higgins and Gill 2010). Farming could also create regional Moran effects independently of climate through national-scale, policy-driven changes in farm management or land use. For example, Paradis et al. (2000) found farmland birds in the United Kingdom had higher spatial synchrony than woodland birds and suggested the cause may be shifts in farm management driven by national agricultural policy. Other potential causes of regional changes in agricultural management include cultural and/or demographic shifts. While documenting spatial synchrony is important on its own due to its relevance to metapopulation persistence (i.e., metapopulations with correlated sub-populations are more extinction prone; Hanski and Woiwod 1993; Earn et al. 2000), the search for causation is equally important as conservation biologists can also benefit from identifying population drivers that can be addressed by management and policy.

In addition to Moran effects, spatial synchrony can be caused by trophic interactions (e.g., spatially synchronous predator or prey dynamics) and dispersal, and it is sometimes possible to disentangle these three main causes. Dispersal- and predator-driven spatial synchrony are typically less spatially extensive than Moran effects (Ims and Adreassen 2000; Michel et al. 2016). Furthermore, dispersal is mostly detectable at a time lag due to interannual natal-dispersal (Martin et al. 2017), and, in birds, mean dispersal distance has shown only a weak correlation with non-lagged spatial synchrony, and only at the local scale (i.e., after removing regional population trends; Paradis et al. 2000). Concordance in patterns of spatial synchrony across multiple species in a guild can be used to provide further evidence for common environmental drivers (Michel et al. 2016). Thus, for species such as grassland birds that are highly sensitive to climate and other environmental fluctuations (Pearce-Higgins et al. 2010; Zuckerberg et al. 2018) we

expect Moran and/or related trophic effects, to be the primary cause of within-year synchrony patterns observed at larger scales (> 100 km).

Mapping the intensity of local spatial synchrony (usually measured as mean correlation to a certain distance) is necessary to identify geographic areas of high, low, or changing spatial synchrony, and can be additionally useful in teasing apart potential causality (Hanski and Woiwod 1993; Michel et al. 2016; Defriez and Reuman 2017a,b; Walter et al. 2017). The causes of these 'geographies of synchrony' can include spatial patterns in the intensity of population drivers (e.g., climate, predators, or land use gradients) or in dispersal (e.g., due to barriers), as well as spatial patterns in a population's responses to these factors (e.g., variation in density dependence; Walter et al. 2017). From a conservation perspective, if dispersal-based spatial synchrony is thought to be minimal, we can use temporally shifting geographies of spatial synchrony as a lens to 'image' areas of increasing impacts of external drivers. From a metapopulation perspective, these increases would be relevant to conservation efforts whether they are due to shifts in the environmental drivers or in the population's sensitivity to them. While geographies of synchrony have been previously leveraged to identify regions of interest for guilds of conservation concern (Michel et al. 2016), temporal changes in this geography have not to our knowledge.

Here we examine decadal changes in geographies of spatial synchrony for 19 species of grassland birds (Fig. 1), a guild of considerable conservation concern known to be sensitive to regional anthropogenic drivers. Our objectives were to 1) quantify the average change in spatial synchrony for each species across their North American ranges, 2) investigate species traits associated with these changes, 3) map changes in synchrony for all species and combine maps to reveal regional guild-wide 'hotspots', and 4) investigate these hotspots further to determine which species were driving patterns

observed. As potential climatic and agricultural drivers of spatial synchrony in this group have increased in intensity in recent decades (Askins et al. 2007; Koenig and Liebhold 2016; Zuckerberg et al. 2018), we hypothesized that grassland birds would show an overall increase in the intensity of spatial synchrony from the first half of North American Breeding Bird survey (1966-1991) to the second half (1992-2017). We further reasoned that hotspots of multi-species increases in spatial synchrony would highlight potential regions of conservation interest, setting the stage for future investigations into mechanisms and ultimately mitigation efforts.

METHODS

Study Area and Data

To examine spatial synchrony in grassland bird species, we used data from of the North American Breeding Bird Survey (BBS), including the contiguous 48 United States and extending to the northern extent of the survey in Canada (~50-55 N latitude; Sauer et al. 2017; Pardieck et al. 2018). These data consisted of > 5 million counts of bird species encountered by surveyors along > 5000 survey routes collected over a 52-year period (1966-2017). Survey routes are ~40 km (25 mi) long with 50 stops at which 3-min counts are performed and summed to produce a single route-level count per species per route per year. The following procedures to estimate spatial synchrony were repeated for two 26-year subsets of the BBS data (1966-1991 and 1992-2017) and for each of the 30 species (Supporting Information) classified as grassland habitat specialists by the BBS (Sauer et al. 2017); 11 of these species were later excluded as they had insufficient data to perform synchrony analyses (see Data Processing and Supporting Information).

Data Processing

We chose to aggregate population data into a 2° latitude x 2° longitude grid to reduce the influence of observer effects and measurement error (mean area: 36,267 km^2 · cell^{-1}, range: 29,192–43,596 km^2). Preliminary explorations with a 1° x 1° grid revealed similar patterns of spatial synchrony (i.e., decay with distance), but a weaker signal evidenced by lower Pearson correlation coefficients. To aggregate data, raw counts were averaged to produce time series of annual abundance data per grid cell. We excluded cells that did not contain 1) at least one route with ≥ 10 years of data, and 2) at least two routes containing the species of interest (after Michel et al. 2016). We further excluded those with ≥ 5 years of zero average counts (i.e., 20-25%; after Martin et al. 2017). Average count data were then log(x+1) transformed and detrended by extracting the residuals of a first-order autoregressive equation fit to each series (Koenig and Liebhold 2016).

Quantifying shifting synchrony

We calculated pairwise Pearson correlations (r) between all grid cells excluding those with n < 20 years. We then used a 400 km moving window at each cell to compute and map mean r, what we hereafter refer to as 'local spatial synchrony' (Walter et al. 2017). Four hundred km was chosen as an appropriate distance to compute average pairwise r as this represents an average of all first-order adjacent grid cells including diagonals. Plotting all pairwise r values to visualize the decay of synchrony with distance also confirmed that 400 km was an intermediate distance for most species, making it a reasonable basis for comparing across multiple species. Grid cells with no neighbors were necessarily dropped during this step. To visualize changes over time, we next created change maps for each species by subtracting local spatial synchrony values in corresponding grid cells of the 'recent' and 'historical' maps (i.e., 1992-2017 minus 1966-

1991). Within each species, grid cells not shared by the two time periods were necessarily dropped during this step.

Due to the exclusion of grid cells at each step, 11 of the less-abundant species from the original BBS list of 30 grassland specialist birds ended up with 0-2 grid cells in the final change map and were excluded from further analysis (Supporting Information). The remaining 19 species (Fig. 1; Supporting Information) had change data or 4-129 grid cells (mean = 52). Mean change in local spatial synchrony and a boot-strapped 95% confidence interval were computed based on these grid cell values for each species. A linear mixed-effect model with a random effect of species and a fixed intercept was used to estimate the average of change in synchrony (± 95 C.I.) across all species.

We hypothesized that variation in temporal changes in synchrony among species may be associated with species-level traits including body mass (log-transformed), phenology (early vs. late nesters), or migratory status (short-distance vs. neo-tropical migrants). We derived body mass and phenology information from Birds of North America (Rodewald 2019), classifying nesting phenology as 'early' (n = 9 species) or 'late' (n = 10) based on whether peak egg laying begins before or after 15 May. Migratory status was taken from BBS guild classifications (Sauer et al. 2017), except for Ring-necked Pheasant (non-migratory) which was lumped with short-distance migrants for this analysis (n = 12 short-distance, 7 neotropical migrant species; Supporting Information). The dependent variable in this analysis was the average change in synchrony by species, weighted by the sample size of grid cells. Five weighted linear regression models were evaluated: three that each contained one of the independent variables, plus a null model with an intercept only and a global model containing all variables. Model performance was evaluated based on AIC_c, effect size (slope) and

confidence intervals, and R^2. All analyses were performed in R (v. 3.5.1; R Core Team 2018).

Geography of guild-level patterns

To view potential guild-level patterns of shifting spatial synchrony, we averaged the final change maps across all species retaining only grid cells where at least 3 of the 19 species (Fig. 1; Supporting Information) were represented. To identify 'hotspots' or regions of consistently positive or negative mean change we used the Local Moran's I procedure with an alpha cut-off of 0.05 (program GeoDa; Anselin et al. 2006). To better understand which species were contributing to these regions, we tallied the number of cells occupied by each species within each hotspot and plotted their mean shifts in synchrony by grid cell within the cluster.

RESULTS

Quantifying shifting synchrony

Fifteen of 19 species (79%; Fig. 1) had increasing and four species (21%) had decreasing estimates of mean change in local spatial synchrony (Δr). Estimates for nine of the 19 species were statistically significant (i.e., confidence intervals did not overlap zero), eight (89%) of which showed significant increases: Long-billed Curlew ($\Delta r = 0.17$), Cassin's Sparrow (0.16), Sedge Wren (0.12), Baird's Sparrow (0.11), Lark Bunting (0.09), Dickcissel (0.09), Western Meadowlark (0.05), and Savannah Sparrow (0.04) (Fig. 1; Supporting Information). Eastern Meadowlark was the only species to show a significant decrease in local spatial synchrony ($\Delta r = -0.07$). The grand mean across all species was an increase in r of 0.04 (95% C.I.: 0.01, 0.07).

Variation among species

Weighted regression revealed no clear evidence that body mass or migratory status were associated with variation in synchrony change among species (Supporting Information). The model containing nesting phenology (adjusted R^2 = 13%; Fig. 2) performed best but did not represent a dramatic improvement over the null model (ΔAIC_c = 0.91). This model predicted a 0.04 higher mean Δr in later-nesting relative to earlier-nesting species (beta = 0.042, SE = 0.022; Fig. 2). None of the remaining models performed as well (ΔAIC_c > 2.52).

Geography of guild-level patterns

Maps of local spatial synchrony and Δr for each species individually are available as supplemental materials (Supporting Information). The map representing average change in spatial synchrony for all 19 species combined contained 145 grid cells ranging from -0.25 to +0.21 (Fig. 3). Hotspot detection (local Moran's I) analysis revealed one major region of increasing synchrony covering a ~522,000 km^2 region (13 grid cells) in the southern Great Plains. This region also coincides closely with the Southcentral Semiarid Prairies ecoregion of Omernik and Griffith (2014). One additional hotspot of synchrony increase consisted of a single grid cell in southern Manitoba. Species that most contributed to the pattern in the Great Plains hotspot (i.e., occurred in ≥ 50% of cells and generally increased) included Horned Lark (increasing in 7 of 10 cells), Cassin's Sparrow (9 of 10), Western Meadowlark (10 of 10), Dickcissel (9 of 9), and Grasshopper Sparrow (6 of 7). Most, but not all, species increased in synchrony within this region: 8 of 12 species had median change values > 0 (Fig. 4).

Similarly, one major and one minor decreasing cluster were identified, both in the Northeast (12 and 1 cells, respectively; Fig. 3). The major decreasing cluster covers

~433,000 km^2 from southern Ontario through New York, Pennsylvania, Maryland, and Delaware. The smaller (single-cell) decreasing cluster is in Nova Scotia. Species most contributing to the decreasing pattern in the larger cluster include Eastern Meadowlark (decreasing in 10 of 12 cells), Vesper Sparrow (7 of 8), Grasshopper Sparrow (6 of 6), Savannah Sparrow (6 of 10), and Horned Lark (5 of 6). Again, most but not all species decreased in synchrony within this region; 8 of 9 species had median change values < 0 (Fig. 4).

DISCUSSION

The geography of spatial synchrony represents a useful addition to the conservation planning toolbox because it can reveal areas of metapopulation vulnerability and of spatially extensive population drivers . Examining decadal changes in these patterns takes this one step further by revealing potential regions of increasing or decreasing impact or vulnerability. We found an overall increase in the range-wide spatial synchrony of grassland bird populations over the survey period (1966-2017), though some variation existed among species (Fig. 1). Geographic variation also existed, and we identified one region of generally increasing spatial synchrony (the southern Great Plains) and one of decreasing synchrony (the Northeast). Mechanisms for these common changes remain unclear, though candidates in the Great Plains region include intensification of agricultural practices as well as increasing annual variance in precipitation.

Quantifying shifting synchrony

That grassland birds are generally increasing in spatial synchrony agrees with other recent work on North American birds (Koenig and Liebhold 2016) that found a 50-year

increase in spatial synchrony in winter abundance in ~ 65% of 49 species studied. This change corresponded with a continental-scale increase in the spatial synchrony of annual maximum temperatures. Similarly, decadal changes in the spatial synchrony of aphid emergence timing was found in the U.K. and was strongly coherent with winter temperature fluctuations (Sheppard et al. 2016). While a mechanism was not definitively identified in either study, it is a general concern that populations may be 1) increasingly responding to large-scale anthropogenic shifts in climate patterns; and 2) becoming more synchronous in ways that increase vulnerability to metapopulation extinctions or outbreaks (e.g., for pest species; Sheppard et al. 2016). For grassland birds that have experienced large-scale habitat fragmentation, correlated fluctuations caused by Moran effects could have real conservation implications. Populations with simultaneous low-points have lower likelihood of demographic rescue and therefore increased chances of metapopulation extinction (Earn et al. 2000; Hufbauer et al. 2015). This is particularly a concern if we are only witnessing the beginning of more-extreme increases in synchrony tracking projected climate change. Research into mechanisms causing variation in synchrony changes among species is needed to better understand future trajectories of synchrony and their conservation implications. This could be a valuable complement to research into widespread shifts in phenology and other impacts driven by climate change (e.g., Socolar et al. 2017).

Variation among species

Though most grassland birds share the traits of a declining population size and nesting on or near the ground (Sauer et al. 2017), there is considerable variation in other traits including evolutionary lineage, life history, breeding phenology, and migratory status. Contrasting patterns of changes in spatial synchrony among species could theoretically be explained by vulnerability to common environmental changes

experienced by these groups. Our finding that phenology best predicted overall change in synchrony could result from sensitivities to climate or farming activities during vulnerable life stages such as nesting or post-fledging. Intensification of farming has been linked to large-scale declines in grassland-nesting species globally, stemming from the destruction of nests by farm machinery as well as general habitat loss and degradation (Donald et al. 2001; Askins et al. 2007; Azpiroz et al. 2012). Nest losses due to agricultural activities depend on timing of management and would therefore be expected to differentially affect species with different nesting phenologies. A regional shift in average harvest or other management timing that disproportionately affected later nesting species, for example, could cause the patterns we observed. Seasonal climate stresses – e.g., regional droughts that affect food availability during sensitive periods – also have the potential to cause spatial synchrony. Populations of grassland species can be affected by annual climate, sometimes in contrasting ways (Gorzo et al. 2016; Wilson et al. 2018; Zuckerberg et al. 2018), which could explain some of the variation in synchrony observed among species. For migratory species, agricultural or climatic conditions on common wintering grounds (e.g., in the Chihuahua grasslands or the southeastern U.S.; Pool et al. 2014; Macías-Duarte et al. 2017, Woodworth et al. 2017) also have the potential to cause spatial synchrony on the breeding grounds, especially where strong migratory connectivity exists (Marra et al. 2019). Such 'connectivity synchrony' is an intriguing possibility that has not been considered previously to our knowledge (Walter et al. 2017) but is highly probable in migratory species with high site fidelity. For example, the severity of winter in the southeastern U.S. strongly predicts Savannah Sparrow population fluctuations on their summer home in New Brunswick, Canada (Woodworth et al. 2017). However, the lack of differences between long- and short-distance migrant species observed in our study are more suggestive of effects on shared breeding grounds.

Geography of guild-level patterns

While patterns averaged over the range of a species are instructive, at the same time they can mask hot spots of increasing or decreasing synchrony that could cancel each other out if aggregated to a larger scale (Walter et al. 2017). For example, in the current study, Grasshopper Sparrow and Horned Lark were both found to be increasing in synchrony in the southern Great Plains but decreasing in the Northeast (Fig. 4). This is a major benefit of the 'geography of synchrony' approach (Walter et al. 2017), as well as focusing on the guild-level, highlighting regions in which multiple members of a guild are experiencing high or low spatial synchrony. For example, distinct geographical zonation of spatial synchrony exists within individual aerial insectivore bird species in North America (Michel et al. 2016). However, these zones do not match geographically as would be expected if species were responding to the same regional driver (e.g., insect populations), thus suggesting individualistic reasons for population declines in aerial insectivores. Our analysis took this further by combining the geographic and guild-level approaches (e.g., Michel et al. 2016) with efforts to document decadal changes in synchrony (e.g., Koenig and Liebhold 2016), thus mapping decadal changes in geographies of synchrony at the guild level. We are not aware of any other applications of this 'shifting geography of spatial synchrony' approach for conservation and know of only one other instance in which it was used for any purpose (Walter et al. 2017).

Of the two regions of changing spatial synchrony identified, the increasing pattern in the southern Great Plains may have the largest conservation implications because it 1) contains a larger share of historical and current grassland bird populations than the Northeast (Sauer et al. 2017), and 2) has experienced an increase in spatial synchrony with associated negative conservation implications. The pattern of increasingly synchronous populations in this region is driven primarily by increases in six

passerine species representing four families (Fig. 4). If increases in spatial synchrony in these species is driven by increases in a common environmental mechanism – e.g., an agricultural and/or climatic Moran effect – this raises the question of which factors are the likely candidates.

The area of increasing synchrony in the southern Great Plains (Fig. 3) lies within the Southcentral Semiarid Prairies ecoregion and overlaps most broadly with two sub-regions known as the Western High Plains and the Southwestern Tablelands (Omernik and Griffith 2014). Both are heavily agriculturalized, with almost all non-urban land in irrigated row crops (from water in the Ogallala aquifer) or in public and private grazing lands (Taylor et al. 2015). The Conservation Reserve Program (CRP), which involves planting croplands to perennial grasses and taking them out of production, has acted as an important driver of land use in the region since the mid-1980s. This program drives a "cyclical change that involves the conversion of grassland/shrubland to mechanically disturbed and then back to grassland/shrubland" (Taylor et al. 2015, p. 12) and has the potential to cause a kind of agricultural policy Moran effect, like that proposed for farmland birds in the United Kingdom (Paradis et al. 2000). Indeed, rotation between grassland/shrubland and row crop agriculture was the primary land use change in both ecoregions between 1973-2000, with the net amount of grassland increasing slightly (Taylor et al. 2015).

The southern Great Plains is also characterized by high longitudinal variation in precipitation spanning ~10-35 inches per year, as well as extreme annual variation in precipitation (Christian et al. 2015). Notably, drought-pluvial dipoles, a phenomenon in which extreme dry years are followed immediately by extremely wet years, have been found to be increasing in recent decades (ibid.). Some grassland species – including Lark Bunting and Grasshopper Sparrow, which both increased in synchrony in the region

– show strong population responses to precipitation (Gorzo et al. 2016; Wilson et al.
2018). Given these factors, increased fluctuations in precipitation (and perhaps resulting
effects on habitat structure and food resources) are also a plausible cause for increased
synchrony in the region. Furthermore, climatic dipoles – generally referring to 'seesaw'
dynamics between climate extremes – have been associated with spatially synchronous
population dynamics elsewhere such as winter finch irruptions in North America (Strong
et al. 2015) and malaria outbreaks in East Africa (Chaves et al. 2012).

From geography of synchrony to geography of mechanism

Our approach leveraged temporal shifts in the geography of spatial synchrony to
highlight previously hidden areas of potential conservation concern. A logical extension
of this 'shifting geography of synchrony' approach would be to attempt the
decomposition of these patterns by searching for 'geographies of mechanism'. For
example, clues to multi-species Moran effects can be found by mapping concordance in
cross-synchrony, or correlated fluctuations between species in the same locations
(Michel et al. 2016). Extending this approach to examine temporal changes in these
patterns could also be revelatory. Even more explicit in terms of mechanisms would be
to directly examine the geography of correlation strength between population fluctuations
and relevant weather phenomena thought to be the most likely drivers of a Moran effect.
This is easily accomplished given the ready availability of spatiotemporal climate data.
As density dependence within populations can also affect geographical patterns of
synchrony (Hanski and Woiwod 1993; Walter et al. 2017), mapping measures of density
dependence (e.g., those used in Brook and Bradshaw 2006) may also bear fruit in
teasing apart causation. While revealing 'geographies of correlation' won't necessarily
yield 'geographies of causation', the more information we have regarding the many

potential contributors to spatial synchrony the closer we will get to a convincing synthesis of the evidence.

Ultimately, the effectiveness of spatial synchrony as a conservation tool will rest in part on our ability to unveil the identities of regional population drivers that it helps us locate; and also the extent to which these drivers can be addressed by policy and management. Changes in regional agricultural management can be met with incentive programs or other policy instruments, whereas regional population stresses caused by increasing drought intensity are not as easy to address. Similarly, the risks posed by the correlated fluctuations themselves (e.g., reduced rescue effects, increased population variability) have few easy solutions, although increasing connectivity among regions through habitat conservation and restoration efforts would likely help. Regardless if the causes of spatial synchrony remain hidden or intractable, documenting landscapes of synchrony remains a useful exercise to inform existing spatial conservation planning efforts, and to highlight areas to monitor and mine for potential ecological and conservation-relevant insights.

AKNOWLEDGEMENTS

SUPPORTING INFORMATION

A full list of grassland bird species included in this study with scientific names, along with data (Appendix S1) and model output (Appendix S2) for the trait-based analysis are

available online. Also online are maps of the species-specific mean local spatial

synchrony in the periods 1966-1991 (Appendix S3) and 1992-2017 (Appendix S4), and

species-specific maps of the change in spatial synchrony (Appendix S5). The authors

are solely responsible for the content and functionality of these materials. Queries (other

than absence of the material) should be directed to the corresponding author.

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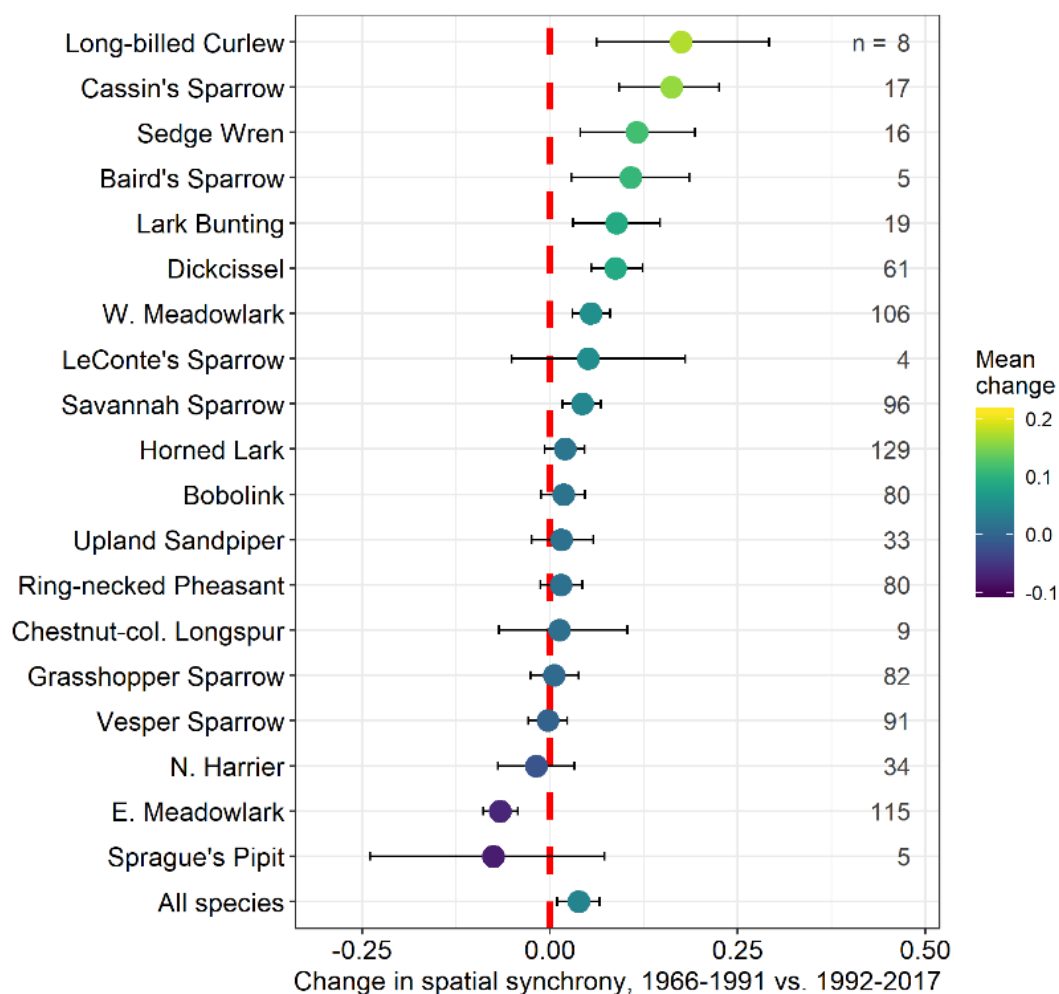
Figures

Figure 1. Changes in spatial synchrony in grassland birds between the periods 1966-1991 and 1992-2017. Spatial synchrony was measured as the mean cross-correlation (Pearson coefficient) of populations within 400 km. Sample sizes represent the number of 2 x 2 degree grid cells the mean estimate is based on. Scientific names are available online (Supporting Information).
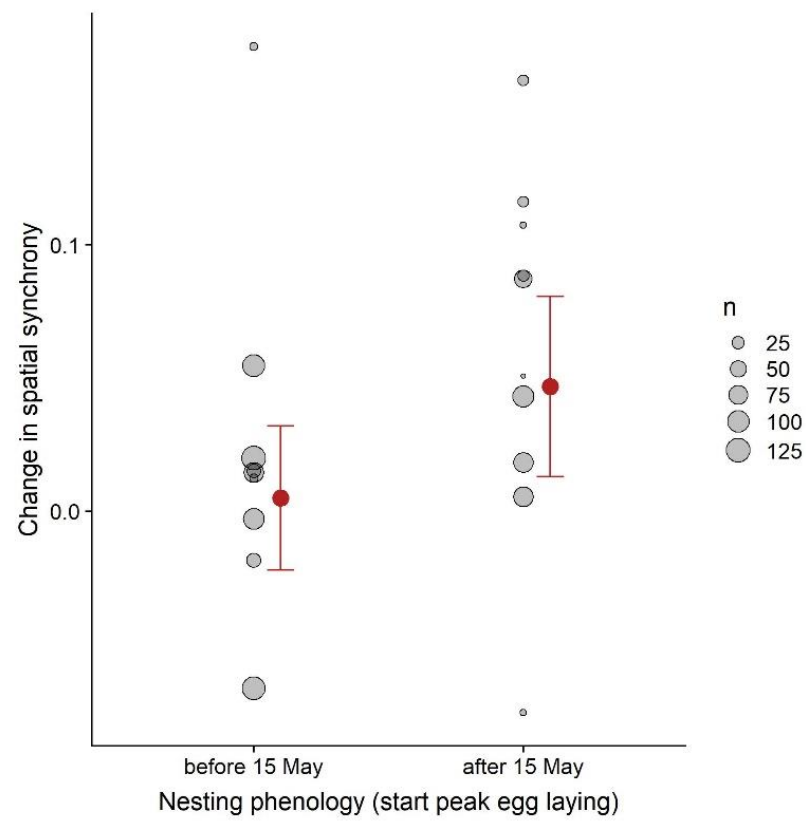
Figure 2. Change in spatial synchrony in grassland birds (1966-1991 vs. 1992-2017) in relation to nesting phenology. Species were classified by whether their peak egg-laying period begins before or after 15 May.
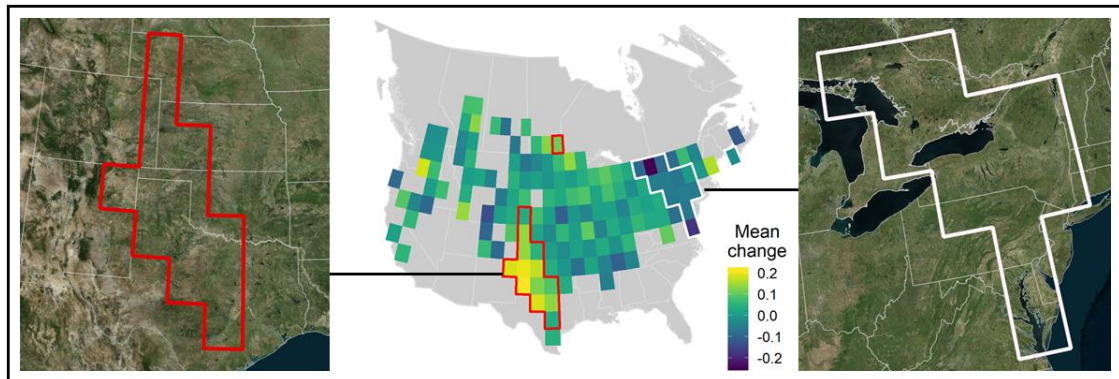
Figure 3. The geography of decadal shifts in spatial synchrony averaged across 19 grassland bird species (see Fig. 1). Grid cells show the mean change in spatial synchrony (1966-1991 vs. 1992-2017) for grid cells with estimates for at least three species. 'Hotspots' of increasing and decreasing spatial synchrony (red and white outlines, respectively) were identified using local Moran's I analysis (alpha = 0.05).
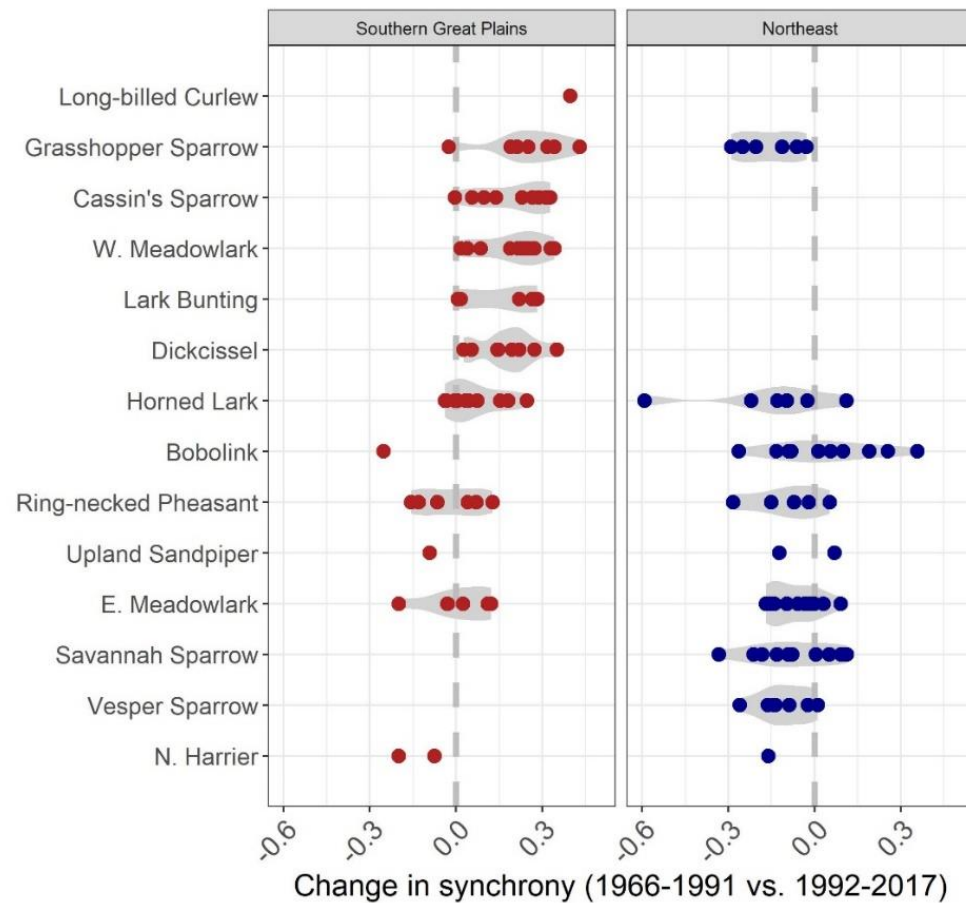
Figure 4. Species contributions to the two main 'hotspots' of changing spatial synchrony shown in Fig. 3. Each point represents the change in spatial synchrony (1966-1991 vs. 1992-2017) in that species in a grid cell within the identified region. Horned Lark, Cassin's Sparrow, Western Meadowlark, Dickcissel, and Grasshopper Sparrow were the main species contributing to the pattern in the increasing region; main contributors to the pattern in the decreasing region include Eastern Meadowlark, Vesper Sparrow, Grasshopper Sparrow, Savannah Sparrow, and Horned Lark (see Results). Scientific names are available online (Supporting Information).

SUPPORTING INFORMATION

Appendix S1. List of species considered grassland specialists by the North American Breeding Bird Survey along with information used in the modelling of change in spatial synchrony based on species traits.

Appendix S2. Model results for the analysis of change in spatial synchrony based on species traits.

Appendix S3. The geography of mean local spatial synchrony for 22 species with adequate data during the period 1966-1991. See Appendix S1 for abbreviations.

Appendix S4. The geography of mean local spatial synchrony for 23 species with adequate data during the period 1992-2017. See Appendix S1 for abbreviations.

Appendix S5. The geography of mean changes in local spatial synchrony (Δr) for 21 species with adequate data between the periods 1966-1991 and 1992-2017. Two species (McCown's Longspur [MCCO] and Sharp-tailed Grouse [STGR]) were excluded from the final analysis as they had only two grid cells with adequate data. See Appendix S1 for abbreviations.

Appendix S1. List of species considered grassland specialists by the North American Breeding Bird Survey along with information used in the modelling of change in spatial synchrony based on species traits.

Species[a]	Abrev.	Mean Δr (95% C.I.)[b]	Grid Cells[c]	Mig.[d]	Phen.[e]	Mass (g)
Long-billed curlew (*Numenius americanus*)	LBCU	0.17 (0.05, 0.29)	8	N	early	699.4
Cassin's sparrow (*Aimophila cassinii*)	CASP	0.16 (0.1, 0.23)	17	S	late	18.3
Sedge wren (*Cistothorus platensis*)	SEWR	0.12 (0.04, 0.19)	16	S	late	8.0
Baird's sparrow (*Ammodramus bairdii*)	BAIS	0.11 (0.02, 0.19)	5	N	late	18.5
Lark bunting (*Calamospiza melanocorys*)	LARB	0.09 (0.03, 0.15)	19	N	late	37.2
Dickcissel (*Spiza americana*)	DICK	0.09 (0.05, 0.12)	61	N	late	26.9
Western meadowlark (*Sturnella neglecta*)	WEME	0.05 (0.03, 0.08)	106	S	early	97.7
Le conte's sparrow (*Ammodramus leconteii*)	LESP	0.05 (-0.05, 0.18)	4	S	late	13.1
Savannah sparrow (*Passerculus sandwichensis*)	SAVS	0.04 (0.02, 0.07)	96	S	late	19.7
Horned lark (*Eremophila alpestris*)	HOLA	0.02 (-0.00, 0.05)	129	S	early	107.9
Bobolink (*Dolichonyx oryzivorus*)	BOBO	0.02 (-0.01, 0.05)	80	N	late	30.9
Upland sandpiper (*Bartramia longicauda*)	UPSA	0.02 (-0.02, 0.06)	33	N	early	157.5
Ring-necked pheasant (*Phasianus colchicus*)	RNEP	0.01 (-0.01, 0.04)	80	S	early	1090.0
Chestnut-col. Longspur (*Calcarius ornatus*)	CCLO	0.01 (-0.07, 0.1)	9	S	early	20.3
Grasshopper sparrow (*Ammodramus savannarum*)	GRSP	0.01 (-0.03, 0.04)	82	N	late	18.0
Vesper sparrow (*Pooecetes gramineus*)	VESP	0.00 (-0.03, 0.02)	91	S	early	25.7
Northern harrier (*Circus cyaneus*)	NOHA	-0.02 (-0.07, 0.03)	34	S	early	424.5
Eastern meadowlark (*Sturnella magna*)	EAME	-0.07 (-0.09, -0.04)	115	S	early	111.7
Sprague's pipit (*Anthus spragueii*)	SPPI	-0.08 (-0.22, 0.07)	5	S	late	23.8
Botteri's sparrow (*Aimophila botterii*)	BOSP	-	0	-	-	-
Common barn-owl (*Tyto alba*)	BANO	-	0	-	-	-
Ferruginous hawk (*Buteo regalis*)	FEHA	-	0	-	-	-
Greater prairie-chicken (*Tympanuchus cupido*)	GRPC	-	0	-	-	-
Henslow's sparrow (*Ammodramus henslowii*)	HESP	-	0	-	-	-

Appendix S1. (continued)

Species[a]	Abrev.	Mean Δr (95% C.I.)[b]	Grid Cells[c]	Mig.[d]	Phen.[e]	Mass (g)
Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*)	LEPC	-	0	-	-	-
McCown's longspur (*Calcarius mccownii*)	MCCO	-	2	-	-	-
Mountain plover (*Charadrius montanus*)	MOPL	-	0	-	-	-
Sharp-tailed grouse (*Tympanuchus phasianellus*)	STGR	-	2	-	-	-
Short-eared owl (*Asio flammeus*)	SEOW	-	0	-	-	-
White-tailed Hawk (*Buteo albicaudatus*)	WTHA	-	0	-	-	-

[a]Only the 19 species used in the final analysis have trait information.
[b]Mean change in local spatial synchrony with bootstrapped 95% confidence intervals.
[c]Number of grid cells with an estimate of change in local spatial synchrony.
[d]Migratory status: short = short-distance migrant; neo = neo-tropical migrant
[e]Nesting phenology: early = peak egg laying begins before 15 May; late = after 15 May

Appendix S2. Model results for the analysis of change in spatial synchrony based on species traits.

Model	Adj. R^2	df[a]	ΔAIC_c[b]	Parameter	Coefficient (95% C.I.)
Δr ~ Phenology	13%	3	0	Intercept	0.005 (-0.023, 0.034)
				Phenology (late)	0.042 (-0.004, 0.087)
Δr ~ 1 (intercept only)	NA	2	0.91	Intercept	0.021 (-0.003, 0.045)
Δr ~ log(Mass)	1%	3	2.52	Intercept	0.062 (-0.022, 0.147)
				log(Mass)	-0.010 (-0.029, 0.010)
Δr ~ Migratory status	0%	3	2.62	Intercept	0.039 (-0.005, 0.084)
				Migratory status (short)	-0.026 (-0.078, 0.027)
Δr ~ log(Mass) + Migratory status + Phenology	2%	5	6.89	Intercept	-0.018 (0.179, 0.142)
				log(Mass)	0.004 (-0.024, 0.032)
				Migratory status (short)	0.005 (-0.063, 0.073)
				Phenology (late)	0.051 (-0.032, 0.135)

[a]Model degrees of freedom.
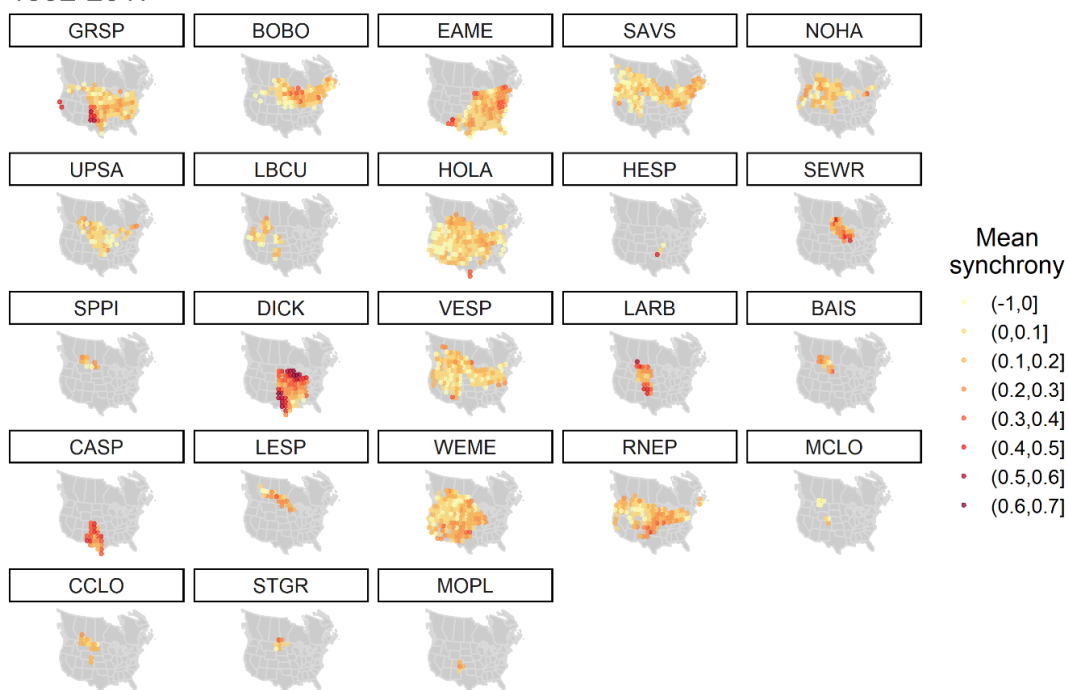
[b]Minimum AIC_c = 47.55

Appendix S3. The geography of mean local spatial synchrony for 22 species with adequate data during the period 1966-1991. See Appendix S1 for abbreviations.

1966-1991
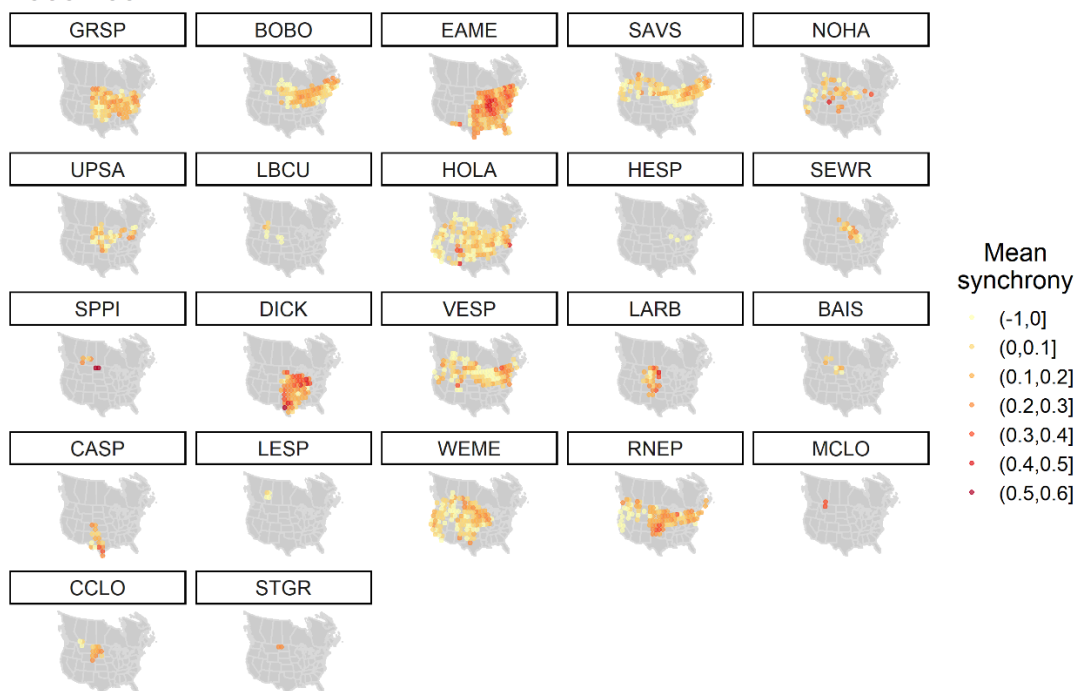
Appendix S4. The geography of mean local spatial synchrony for 23 species with adequate data during the period 1992-2017. See Appendix S1 for abbreviations.

1992-2017

Appendix S5. The geography of mean changes in local spatial synchrony (Δ*r*) for 21 sp
ecies with adequate data between the periods 1966-1991 and 1992-2017. Two species (
McCown's Longspur [MCCO] and Sharp-tailed Grouse [STGR]) were excluded from the
final analysis as they had only two grid cells with adequate data. See Appendix S1 for ab
breviations.

1966-1991 vs. 1992-2017